**Ravens At Play: The Social and Developmental Importance of Item-Caching Play Behavior in Ravens**

 The sources are organized according to the development of caching behavior, object play as a phenomenon, item caching as a phenomenon, and the specific influence of social context on caching behavior. The categories are intended to go from most broad (ontogeny) to most specific (context and detailed accounts of the behavior). However, some categories are relatively interchangeable in terms of broadness.

 **Behavioral Ontogeny and Development**

Bugnyar, T., Stöwe, M., & Heinrich, B. (2007). The ontogeny of caching in ravens, *Corvus corax*. *Animal Behaviour*, *74*(4), 757–767. <https://doi.org/10.1016/j.anbehav.2006.08.019>

*Summary:* Previous studies found that corvid cache retrieval develops synchronously with the awareness of object permanence and the hippocampus. Additionally, corvids were known to develop stage five object permanence faster than non-caching birds. This trend suggests possible selective pressure to develop object permanence before independence. Previous studies on corvids also determined that object permanence develops in steps: no attempt to search for a concealed object (stage 1), tracking of the item’s movement (stage 2), recovery of a partially hidden item (stage 3), recovery of a fully concealed item (stage 4), retrieval of an item visibly moved from one hiding place to another (step 4), and the same with an item which has been invisibly moved (stage 5). They also cache not only food but small non-food items. Bugnyar observed captive ravens throughout development to determine whether object and food caching differ, and study the development of long-term memory. Bugnyar and company gave the ravens cachable food and high-value items. The locations and methods of caching were recorded. Complex caching (full camouflage of the object away from conspecifics) developed two months post-fledging and mirrored the development of object permanence. Level five object permanence and caching behaviors appeared pre-independence and were applied equally to object and food caches. Differences between object and food caching manifested within six months post-fledging—the ravens increased the distance between themselves and conspecifics when caching food. From these observations, Bugnyar and company theorized that the ravens had a value system that prioritized food as a more important resource than items.

*Contribution:* Bugnyar and company’s findings suggest that caching skills are essential to learn before adulthood (corroborated by the fact that ravens cache objects less as they approach maturity). Hence, item caching in juvenile ravens is vital to developing foraging behaviors, and should be encouraged in young birds. Additionally, ravens have the intelligence to place different values on items; could this value system also apply to social relationships? An avenue for future research: Is the observed hypothetical value system universal or individual?

Heinrich, B. (2011). Conflict, cooperation, and cognition in the common raven. *Advances in the Study of Behavior*, *43*, 189–237. <https://doi.org/10.1016/B978-0-12-380896-7.00004-6>

*Summary:* Heinrich previously knew that ravens had a complex social system communicated by calls and body language. This secondary article is a summary of Heinrich’s significant experimental findings. Heinrich provides an overview of his previous research papers about social interactions within raven groups, particularly in feeding situations. His research found that, although ravens are social animals, they do not ‘flock’ in the way that smaller songbirds do (Heinrich, 1988; Heinrich et al. 1994). Permanent ties tend to be between bonded pairs (Marzluff and Heinrich, 1991). More temporary bonds form in roosts, which Heinrich theorizes provide both safety and a means of transmitting information about potential food sources. The social roost theory is supported by Heinrich’s observations that uninformed ravens follow informed ravens to food sources (Heinrich, 1988). Rarely, in situations where flocking is beneficial for survival, flocks may form. Agonistic interactions are more likely to occur between those of similar rank than between a higher ranked individual and a bottom-of-the-pack bird, presumably due to the lack of threat from the submissive bird towards the leader’s position. Heinrich overall concludes that although ravens do engage in affiliative behaviors, they do not engage in social interaction with the same flock over their lifespan. However, Heinrich also asserts that ravens have the social intelligence required to learn from conspecifics (eg. In the case of uninformed ravens following others to food).

*Contribution:* Heinrich’s observations that ravens are not constantly associating with either kin or conspecifics suggests that social object play serves a function beyond kinship. Social object play could facilitate the development of sophisticated foraging behaviors in the presence of conspecifics to avoid stealing and losing valuable resources. His observations support the hypothesis that item caching and exploration is more of a learning behavior than simply manifesting a means of social facilitation.

Kaplan, G. (2020). Play behaviour, not tool using, relates to brain mass in a sample of birds. *Scientific Reports*, *10*(1), 20437. <https://doi.org/10.1038/s41598-020-76572-7>

*Summary:* In previous studies, it was assumed that tool use is associated with brain size and cognitive ability; however, in Kaplan’s (2020) review, play behavior (social play behavior in particular) showed positive correlation with overall brain size. Kaplan came to their conclusions by compiling data on brain size, social behavior and tool use in birds from numerous independent experiments on a wide variety of bird species. Kaplan (2020) noted that extended parental care correlated with larger brain mass. Furthermore, Kaplan (2020) noted that stress correlated to a lack of play and enrichment and decreased adult brain size. Kaplan (2020) hypothesized from this data that elaborate play behavior is a by-product of the relative safety associated with long periods of parental care. More energy can be put into exploratory learning and play when food, shelter and protection are guaranteed. Furthermore, the small amounts of stress created during play-fighting may teach young ravens to manage stress as adults. Therefore, Kaplan (2020) concluded that play, as a form of mediated stress (through play-fighting), may relieve stress and allow juvenile ravens to moderate their responses to stressful situations in the future.

*Contribution:* In finding that brain size correlates with play behavior, Kaplan (2020) emphasizes the importance of play to brain development. As such, it is reasonable to theorize that social object play (like item caching) could be a method of social learning. Play also functions to minimize stress to ensure proper neurological development, as it was also found in the review that stress during maturation can stunt this process. Because of this, it is valuable in discussing raven rehabilitation, especially when considering orphaned or injured young ravens.

Miller, R., Bugnyar, T., Pölzl, K., & Schwab, C. (2015). Differences in exploration behaviour in common ravens and carrion crows during development and across social context. *Behavioral Ecology and Sociobiology*, *69*(7), 1209–1220. <https://doi.org/10.1007/s00265-015-1935-8>

*Summary:* Before Miller’s experiments, corvids were known to have neophobic tendencies, and that novel food and object exploration in young animals played a role in the development of foraging habits. Miller and company (2015) designed an experiment to study neophilic and neophobic responses throughout corvid life stages and social situations by exposing wild-born crows and captive-born ravens to novel situations in an aviary familiar to the corvid subjects. These novel situations included small objects which could be manipulated, novel food items, novel and familiar people, and large immovable novel structures. Miller’s experiment also explored how the willingness to explore differs between individual corvids, and corvids in the presence of (usually related) conspecifics. Miller (2015) observed that fledglings in both species interacted the most with novel objects and people. Ravens were more likely to interact with novel people in general. Neophilic and neophobic behaviors changed depending on social context; when in a group, the speed at which novel object interaction occurred decreased. However, the frequency of interaction increased. Miller (2015) hypothesized that this might result from existing dominance hierarchies; dominants could inspire or prevent approach. Miller also concluded that ravens in groups might be less afraid to interact with an unfamiliar object in a group once the first raven has approached due to more protection offered by conspecifics. Further questions could be explored regarding adult corvids—how does novel object interaction change between and within species according to hierarchies, sex, and social context?

*Contribution:* I included this article because it hints at the importance of object play in young ravens as being important for foraging development, and addressed how object manipulation (like item caching) changes with changing social contexts. The article sparked the following subjects I would like to explore in the review: is item caching important in developing dominance/social hierarchies? Is there a difference between birds who item cache as fledglings/juveniles in how they hide high-value food/items, or in their foraging success?

**Avian Object Play (General)**

Bond, A., & Diamond, J. (2003). A comparative analysis of social play in birds. *Behaviour*, *140*(8–9), 1091–1115. <https://doi.org/10.1163/156853903322589650>

*Summary:* This article discusses the occurrence of social play in various species of birds using comparative biology. Data was compiled regarding many different taxa of birds from different primary studies; conclusions were drawn based on comparisons between data sets. They did not gather the data themselves, but used the data from previously conducted studies focusing on avian play behavior to come to their conclusions. The article defines social play as reciprocal play with no consummatory conclusion in the first section. Play behaviors are exaggerated and involve objects or interactions not obviously valuable to either’s survival. Bond and Diamond (2003) recategorized the data according to social play types observed: play chasing, play fighting, play invitations, and social object play. Bond and Diamond (2003) noted that corvids and kakas engaged in the most play behavior (corvids engaging in the most social object play). Both groups regularly played with objects. Bond and Diamond (2003) noted that while brain size was not a causal factor in developing social play, brain size in both parrot and corvid families was greater than what would be expected based on an allometric scale. The brain size-play relationship held in other species in which social play behavior was observed. Both corvids and parrots demonstrated a long juvenile period and extended parental care. Bond and Diamond (2003) theorized that altricial development and larger brain size might be required precursors to social play.

*Contribution:* This article layed the groundwork for the type of developmental history required for social object play in ravens. Object caching, as a learned behavior, would theoretically be impacted by the same processes. By knowing the possible factors leading to the development of social object play, I can apply this information to captive recovering ravens and determine what type of situation might trigger item-caching play behavior.

Stöwe, M., Bugnyar, T., Loretto, M.-C., Schloegl, C., Range, F., & Kotrschal, K. (2006). Novel object exploration in ravens (*Corvus corax*): Effects of social relationships. *Behavioural Processes*, *73*(1), 68–75. <https://doi.org/10.1016/j.beproc.2006.03.015>

*Summary:* Corvids are known to have neophobic tendencies as adults. Stöwe and company (2006) designed an experiment to examine the level of novel object fear (neophobia) in juvenile ravens in different social contexts. The ravens were both hand-reared and wild-caught (removed from nests), and raised in a large aviary with natural perches, substrate, and enrichment such as water baths. The ravens were three months old in the first trial, and six months in the second trial (the age at which they would be independent). The tests were conducted in pairs (a dyad) and lone ravens. Between the early and late trials, Stöwe (2006) noted that the time to interact with novel objects and time spent interacting were not significantly different. However, the older ravens tended to spend longer in close proximity to the novel object. In general, individuals interacted with novel objects faster when alone than when in pairs. In the dyad condition, siblings tended to take longer to approach the object, and spent more time close to companions than in non-sibling dyads. There was no sex difference in time to approach in the solitary trials. However, males in a mixed-sex dyad approached faster and maintained contact longer. In same-sex dyads, the submissive individual approached fastest. Stöwe hypothesized that the tendency to approach slower when in the dyad condition was due to contagious fear, or a risk-reduction method (waiting for others to approach first). Stöwe and company (2006) also hypothesized that dominant individuals were more likely to gain greater rewards from a food source. As a result, Stöwe and company theorized that it would be more advantageous for low-ranking ravens to take risks to offset the reward imbalances.

*Contribution:* This experiment solidified the theory that object interaction is impacted by social context. Item caching, as a social behavior, is also most likely impacted by social context. The experiment also provides evidence that ravens are aware of their social standing and will change their behavior accordingly. It is possible that item caching serves as either a social play behavior, or a means of social learning focused more on the interaction with conspecifics than the item itself.

**Item Caching (General)**

Jacobs, I. F., Osvath, M., Osvath, H., Mioduszewska, B., von Bayern, A. M. P., & Kacelnik, A. (2014). Object caching in corvids: Incidence and significance. *Behavioural Processes*, *102*, 25–32. <https://doi.org/10.1016/j.beproc.2013.12.003>

*Summary:* It was previously assumed that food caching was present in a common corvid ancestor, and indicates similar cognitive ability across caching corvid species. Item caching was not fully understood in terms of cognitive and developmental factors, as it does not fill an obvious biological need. Objects do not appear to be mistaken for food, as ravens preferentially cache bright, colorful items. Jacobs and company (2014) wanted to study the relationship between enhanced cognition and caching and the function of item caching. Jacobs and company (2014) studied jackdaws (non-cachers), ravens (frequent cachers), and crows (rare cachers) in an aviary familiar to the corvid subjects. The corvids were given novel items within 50 meters of a preferred food item. The researchers noted that the jackdaws and crows prioritized the food, but the ravens interacted with the objects first. Object interest waned in ravens and crows in subsequent trials but increased in jackdaws. Ravens had a stronger initial tendency to interact with novel non-food items, which waned with repeated exposure. Researchers hypothesized that this may be because item curiosity serves to provide new information when exploiting new environments. When no new information is available, the benefit of further interaction decreases. These trials were performed with adult birds, making it challenging to examine the developmental importance of item affinity and caching.

*Contribution:* The exploration of novel objects is likely a learning behavior in order to properly exploit new situations, which is important to opportunistic scavengers like ravens. This is an important contribution because it further highlights that object interaction or play is not a mistaken interaction with a presumed food item and is an intentional behavior.

**Impact of Social Circumstance on Caching**

Bugnyar, T., & Heinrich, B. (2006). Pilfering ravens, *Corvus corax*, adjust their behaviour to social context and identity of competitors. *Animal Cognition*, *9*(4), 369–376. <https://doi.org/10.1007/s10071-006-0035-6>

*Summary:* Ravens were previously known to defend food caches by re-caching and through aggressive interactions. Bugnyar and Heinrich’s (2006) were interested in studying the impact of social context on cache theft. Researchers allowed a potential pilferer to observe a cache being made, then observed the pilferer in three situations: alone, in the presence of the dominant cacher, or with another dominant raven who was not the original storer. Bugnyar and Heinrich (2006) noted that the pilferer stole the cache when alone. If the storer remained, the thief pecked at unrelated non-cache locations. The pilfering raven delayed searching at the unattended cache when in the presence of an ignorant conspecific. The researchers hypothesized that this was a deceptive tactic. The pecking as tactical deception was supported by the observation that pilferers will not engage in false searching in the presence of another non-caching dominant individual, and will instead pilfer the food immediately. The researchers suggested that this may have been to avoid giving away the location of the food they were going to steal. Bugnyar and Heinrich (2006) noted that identifying complex deception is difficult, as there are varying levels of intentionality possible. They also proposed that the false ‘searching’ was to avoid dominant interactions—however, the pilferer did not peck with a dominant non-cacher. The researchers theorized that this was tactical deception, and that the ravens likely had the ability to differentiate between types of competitors quickly.

*Contribution:* This article indicates theory of mind in ravens, and an adaptability in behavior which lends credence to the importance of social learning in ravens. Bugnyar and Heinrich (2006) emphasized that caching and pilfering are not simple behaviors mediated by Pavlovian learning. Social intelligence is a learned skill, possibly aided by play behavior such as object caching. It is important for ravens to develop caching skills and properly gauge competitors’ intentions. This could be learned through juvenile item caching and the subsequent interactions of conspecifics with the caches.

Bugnyar, T., Schwab, C., Schloegl, C., Kotrschal, K., & Heinrich, B. (2007). Ravens judge competitors through experience with play caching. *Current Biology*, *17*(20), 1804–1808. <https://doi.org/10.1016/j.cub.2007.09.048>

*Summary:* In non-avian species, play was previously assumed to be a strategy for determining the behaviors of conspecifics in non-survival situations. Ravens were also previously observed caching small inedible items that did not resemble food. To explore the learning function of caching, Bugnyar and company (2007) gave hand-raised ravens small objects to cache. Two people were allowed to interact with the ravens’ caches—one always stole the cached item, while the other inspected it but left it in place. They then provided the ravens with cacheable food. The ravens, when caching items, showed no difference in caching behavior between the thief and the observer. During the subsequent food test the ravens cached more quickly and made greater efforts at hiding the cache behind obstacles when faced with the thief compared to the observer. The researchers theorized that this was a method of ‘testing’ the tendency of conspecifics to raid the hidden item caches. Bugnyar (2007) suggested that they had learned the behavior of each person from the item cache, which had low stakes, then applied it to defend the more valuable food caches better.

*Contribution:* Bugnyar and company (2007) emphasize the importance of social learning in ravens to ensure effective foraging and caching. It provided further support for the theory that the caching of non-food objects allows ravens to learn about the behaviors of other conspecifics to avoid pilfering. Furthermore, it does not support the idea that item caching is a by-product of food caching—the ravens behaved differently between the types of caches. The ravens can differentiate between types of objects and place differing values on them.

Heinrich, B., & Pepper, J. W. (1998). Influence of competitors on caching behaviour in the common raven, *Corvus corax*. *Animal Behaviour*, *56*(5), 1083–1090. <https://doi.org/10.1006/anbe.1998.0906>

*Summary:* Ravens were known to cache food away from conspecifics. To examine caching in the presence of conspecifics, Heinrich and Pepper (1998) placed two male and two female hand-reared ravens (subadults) in an aviary with either one large piece of meat, or many smaller pieces of meat. The different trial types were conducted in both solo and group sessions. Heinrich and Pepper (1998) noted that smaller pieces were cached faster than large piece in both social settings. The pieces were cached fastest in a group setting. The trips were farther from the location of the food in groups. In a second experiment, 21 subadults were either denied food for 24 hours, or allowed to eat normally. All birds were fed and allowed to cache, then put back into an isolated portion of the aviary. Cache retrieval was examined one, 14 and 28 days later. Trials were run with the addition of 40 artificial caches to test whether the ravens were responding to scent cues. The artificial caches were not discovered, making scent cues unlikely. 68% of caches were recovered 24 hours later, 32% two weeks later, and only 7.7% after 28 days. The final experiment tested whether ravens observe others caching. Four hand-reared and one wild raven were housed in an aviary where caching was visible to all subjects. After unsuccessful feeding attempts due to aggressive interactions, Heinrich and Pepper (1998) observed that the wild bird later recovered the caches of the others rather than continuing to approach the communal food pile. Heinrich and Pepper (1998) suggested that ravens use spatial memory to recover theirs, and others’, caches. They also engage in more rapid caching in the presence of competitors, indicating that social context impacts caching behavior. In the final experiment, Heinrich and Pepper (1998) concluded that the wild raven was learning through observation and utilizing long-term memory to pilfer caches.

*Contribution:* Heinrich and Pepper (1998) assert that ravens observe other competitors' caching and feeding behaviors and exploit them. To ensure effective foraging, ravens must learn these cues. I hypothesize that this is through play caching. These learned cues could be learned via the item caching habits of conspecifics during the juvenile stage, and should be encouraged to maximize the success of released subadult and adult ravens during rehabilitation.