

The social suppression of caching in western scrub-jays (*Aphelocoma californica*)

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(Accepted: 16 June 2005)

Summary

This study focussed on the social suppression of caching in 3 groups of western scrub-jays (*Aphelocoma californica*). Each group (3 males and 4 females) were housed in a separate aviary. Only the dominant male and/or his partner cached in each aviary. When the alpha pair was removed from the aviary, however, caching by the beta pair increased significantly. As all subordinate birds cache when housed individually, cache cessation was attributed to social suppression. In each aviary, storers from both the alpha and beta pairs tolerated their partners recovering their caches, but treated all other birds aggressively if they approached a cache site. The storer and their partner tended to move one another's caches around multiple times, possibly making the final location of caches ambiguous. Importantly, caches were only moved around repeatedly on trials where multiple pilfering attempts were made. Western scrub-jays therefore appear to adjust their caching behaviour depending on the risk that observers pose to their caches.

Keywords: corvids, western scrub-jays, social suppression, caching.

Introduction

In many species, individuals cache items for their own future consumption, and also pilfer the caches of conspecifics (Brockmann & Barnard, 1979; Heinrich & Pepper, 1998; Emery & Clayton, 2001). The risk that a storer might have their caches stolen, however, often varies as a function of the

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social environment. For example, in the nuthatch (*Sitta europaea*), storers experience a substantially higher degree of pilferage after caching in the presence of conspecifics, compared to caching in their absence (Carrascal & Moreno, 1993). In parids, the perpetrators of cache theft are generally socially dominant, and therefore able to supplant subordinate individuals (Lahti et al., 1998). It has been suggested that the ability to successfully pilfer the caches of subordinates should result in a preference for dominant animals to reduce investment in their own caches (Brodin et al., 2001). However, the results of studies that have investigated the caching rates of dominant and subordinate birds have been equivocal. While some studies have shown that subordinates cache more than their dominant counterparts (e.g., willow tits, *Parus montanus*, Lahti & Ryttonen, 1996), or have found no effect of dominance rank on caching rates (e.g., willow tits, Lundborg & Brodin, 2003; Carolina chickadees, *Poecile carolinensis*, Pravosudov & Lucas, 2000), others have found that dominants cache more than subordinates (e.g., willow tits, Pravosudov, 1985; Siberian tits, *Parus cinctus*, Pravosudov, 1985; mountain chickadees, *Poecile gambeli*, Pravosudov et al., 2003). Furthermore, a study by Lahti et al. (1998) on willow tits suggested that an individual's caching rate might differ as a result of the immediate social environment. Lahti et al. (1998) found that dominant willow tits cached more than subordinates when in a group. However, when the dominants were removed, subordinate tits increased their caching rate significantly, suggesting that, in the presence of dominants, caching by subordinate willow tits may have been socially suppressed.

Unlike parids, social dominance in corvids is not a reliable indicator of an individual's ability to pilfer another's caches, because individuals use observational spatial memory to steal caches they have observed others make, and can therefore steal caches once the dominant has left the scene (Bednekoff & Balda, 1996a, b; Clayton et al., 2001; Bugnyar & Kotrschal, 2002). Current evidence suggests that the capacity for observational spatial memory might be unique to corvids, with only one anecdotal report to suggest that mammals are able to use memory to pilfer others' caches (*Dipodomys merriami*, Daly et al., 1992), and no evidence that parids are able to do the same (black-capped chickadees, *Parus atricapillus*, Baker et al., 1988; Hitchcock & Sherry, 1995; willow tits, Brodin, 1994). The use of observational spatial memory allows prior observers to accurately recover another's caches at a time when the storer is no longer present. The chance that a potential thief

might oversee a caching event, however, may depend on the social structure of the species in question. In territorial species (e.g., Eurasian jays, *Garrulus glandarius*, Clark's nutcrackers, *Nucifraga columbiana*), storers are unlikely to be observed during caching. By contrast, opportunities to cache alone might be few and far between for those birds that live in colonies (e.g., rooks, *Corvus frugilegus*). Consequently, if colonial corvids cache at all, we might expect them to be particularly sensitive to the risk of cache pilferage.

This study focuses on the caching behaviour of western scrub-jays. Western scrub-jays are generally considered to be semi-territorial (Curry et al., 2002), however, there are several reasons why we might expect this species to be particularly sensitive to cache pilferage. For instance, their close relative the Florida scrub-jay (*Aphelocoma coerulescens*) is known to be a co-operative breeder (Woolfenden & Fitzpatrick, 1984, 1996). In a co-operative breeding system, cache theft between group members might not be detrimental to a storer's fitness, because the food may be used to feed the communal young, however, individuals should prevent intruders stealing their caches. The ability to differentiate between intruders and group mates might facilitate the additional requirement that storers recognise individuals, and assess the risk those individuals pose to their caches. Importantly, not only has Cockburn (1996) suggested that a co-operative social breeding system probably represented the ancestral state of the Corvidae, but co-operative breeding is now known to occur in specific populations of western scrub-jays (Burt & Peterson, 1993).

Social interactions are also common in those populations of western scrub-jays in which breeding pairs defend territories. Although these pairs have a simple social breeding structure, pair members frequently interact with neighboring birds, and commonly tolerate the presence of non-breeders (floaters) in their territory. These, often prolonged, social associations have led to the suggestion that this species might have "more complicated social networks than appear superficially" (Curry et al., 2002, p. 18). Furthermore, territory holders, neighbours and floaters could potentially observe and steal one another's caches, an additional reason why western scrub-jays might be sensitive to the risk of cache pilferage, and might therefore engage in counter-tactics to reduce cache theft.

Several studies have examined the effect of pilferage on a storer's caching strategy. Hampton & Sherry (1994) found that black-capped chickadees avoid caching in sites from which caches are consistently pilfered (but see

Baker & Anderson, 1995). More recently, Clayton et al. (2005) showed that although western scrub-jays prefer to cache worms over peanuts, if over a series of trials storers that find their worm caches are consistently pilfered, they reverse their caching preference and cache progressively more peanuts than worms. In these experiments storers were reacting to cache loss rather than responding to the observed actions of a thief. A study by Preston & Jacobs (2001), however, found that storers who observed conspecifics pilfering their caches switched from scatter-hoarding to larder-hoarding, thus making their caches easier to defend. Similarly, Emery et al. (2004) found that after caching in the presence of an observer, western scrub-jays re-cached items in new sites around their home-cage that were defensible from potential thieves. In addition, after a single pilfering trial, the jays switched their recovery strategy from predominantly checking their caches (i.e., returning to a cache site to see whether the food remained there) to predominantly eating them. This would be an advantageous strategy as checked caches remain susceptible to theft, whereas by eating high-risk items the birds are able to generate internal energetic reserves when the risk of theft is high.

The presence of an observer at caching has, in corvids, been shown to elicit the use of behavioural tactics that might serve to reduce the risk of cache theft. Indeed, corvids avoid caching in areas containing a high density of conspecifics (e.g., rooks, Kallander, 1978; magpies, *Pica pica*, Clarkson et al., 1986), and preferentially cache in sites that are 'out-of-view' of competitors (ravens, Bugnyar & Kotrschal, 2002; western scrub-jays, Dally et al., in press), or that potential thieves might find hard to see (Dally et al., 2004). Moreover, when alone, several corvids have been shown to re-cache items to which the caching event was observed, placing them in new unknown sites (e.g., western scrub-jays, Emery & Clayton, 2001; ravens, Heinrich, 1999; Eurasian jays, Goodwin, 1955). These findings suggest that corvids are not only sensitive to the risk of cache pilferage, but that they use protective tactics which may decrease the ability of competitors to use observational spatial memory to pilfer their caches.

In previous studies on caching and pilfering behaviour in western scrub-jays, transparent partitions have prevented would-be thieves from physically accessing cache sites (Emery & Clayton, 2001; Emery et al., 2004). This is in stark contrast to the natural environment where pilferers have immediate and constant access to the caching arena. In the current study, 3 groups of 7 scrub-jays were tested in an aviary situation, and were therefore able to potentially

store and steal caches. We ran two series of trials to compare the behaviour of dominant and subordinate birds when they were competing for a food resource. In the first series of trials all the birds were present in the aviary, whereas, in the second series of trials, the alpha bird (and its partner) was removed. Based on the finding that in a social group, dominant willow tits cache more than subordinates (Lahti et al., 1998), we predicted that the dominant bird in each aviary would be responsible for the majority of caching events. Moreover, the number of items cached by the beta male was expected to rise significantly upon the dominant's removal, as the beta male would essentially then become the dominant bird. In Lahti et al.'s (1998) experiment on willow tits, female birds were found to be subordinate to males, caching fewer items in less preferred sites. Western scrub-jays, however, form long-term socially monogamous pair bonds, and cache in breeding territories that both partners defend (Curry et al., 2002). We therefore predicted that, where the dominant male had a partner, the female member of the alpha pair might also cache, and that both members of the dominant pair would not only actively defend one another's caches, but also tolerate cache recovery by their partner. By contrast, pair members were expected to engage in tactics that might reduce the ability of conspecifics to use observational spatial memory to pilfer cache sites, perhaps by moving items around repeatedly, potentially making final cache location unclear (Dally et al., in press).

Methods

Subjects & apparatus

Twenty-one sexually mature western scrub-jays (*Aphelocoma californica*; 12 females and 9 males) were tested in this experiment. There were three aviaries, and each contained four females and three males. Two of the aviaries measured 0.7 m wide by 2 m high by 2 m long, and the third 0.7 m wide by 2 m high by 1.6 m long. The aviary floors were covered in a thick layer of sawdust to provide a substrate in which the birds could cache, and a grid made of laminated paper laid on top of the sawdust to divide the floor into individual 10 cm by 10 cm cache sites. The birds were maintained inside at 20–22°C on a 12:12 hour light:dark cycle and a diet of mixed nuts, dog biscuits, various fruits and meats, wax worms and mealworms. The maintenance diet was removed from the aviary the evening before an observation

session (6 pm), to ensure that the jays were mildly hungry during caching the next morning (10 am).

Procedure

(a) Social interactions

Ten 30-min trials were conducted in each of two conditions. In the 'dominant present' condition, all birds were present in the aviary. By contrast, during the 'dominant removed' condition, the dominant male, and where applicable his partner, were removed from the aviary. During a trial the jays often acted aggressively towards one another. These interactions took one of two forms, either a bird would peck a conspecific, or they would fly towards them rapidly displacing them from their perch. The bird that was either pecked or successfully displaced was recorded as having lost that interaction, and the aggressor as having won it. In situations where two birds pecked each other alternately in quick succession, the individual that gave the last peck of the bout was deemed to have won. The number of aggressive interactions that were won or lost by each bird was recorded throughout each trial.

After the first 10 trials ('dominant present' condition) an index of dominance was constructed (see Data analysis). To determine whether there was an effect of social suppression upon the caching rates of subordinate birds, the dominant bird was removed from each aviary and 10 further caching trials conducted ('dominant removed' condition). In two of the aviaries (A and B), the dominant male had formed a partnership with a female bird who was also removed during the ensuing 'dominant removed' condition. These partnerships were identified by the propensity of the female bird to spend a large proportion of time in close proximity to, and share food with, the dominant male. This has been suggested to be a clear indication that an affiliation has developed between adult corvids (de Kort et al., 2003; Emery, 2004).

(b) Caching

During both the 'dominant present' and 'dominant removed' conditions, the caching behaviour of the jays was recorded during each trial. The jays were presented with fifty items of their most preferred food (wax worms), in a 15 cm diameter bowl placed centrally on the aviary floor. Each time food items were cached, the identity of the storing bird was recorded along with the location of the cache site. Similarly, if an item was moved from one site

to another during a trial, the identity of the bird that moved the item, and the location to which the food item was moved, were also recorded.

Data analysis

(a) Social interactions

A dominance index was constructed for the birds in each aviary. The most dominant bird won the greatest proportion of the aggressive interactions in which they were involved, and the most subordinate bird the least. Therefore, the total number of aggressive interactions won by each bird was summed across trials, and divided by the total number of interactions in which they were involved to provide an index of dominance. Birds were ranked from most dominant (highest dominance index) to most subordinate (lowest dominance index).

(b) Caching

A Friedman's ANOVA was conducted to compare the number of caching events that occurred during the 'dominant present' and 'dominant removed' condition for each aviary. Unfortunately, as only one or two birds cached in each aviary it was not possible to correlate dominance rank and the number of times a bird cached. Wilcoxon's paired tests were conducted to compare the number of times the beta males cached in both the 'dominant present' and 'dominant removed' condition. Spearman's rank correlations (Siegel & Castellan, 1988) were also conducted for each aviary to correlate dominance rank with the number of times a bird fed from the food bowl during the 'dominant present' condition, and the order in which they did so. Unfortunately, the sample size in the 'dominant removed' condition (five birds) was too small to perform a statistical correlation of rank and feeding events.

During each trial, storers often cached food in one site before subsequently moving it to a new site. The total number of times caches were moved was recorded for each trial, but, unlike a previous study (Dally et al., in press), it was not possible to determine the mean number of times each cache was moved, because, the number of times a bird cached was recorded, not the number of items cached. This arose because it was difficult to discern exactly how many items a storer took from the food bowl for caching. Spearman's rank correlations were conducted for the total number of times the storers moved a cache during a trial and the number of pilfering attempts

during that trial for aviaries B and C, for both the 'dominant present' and 'dominant removed' conditions. Too few pilfering attempts were made in Aviary A to make statistical analysis possible. Alpha was set at 0.05 and medians and inter-quartile ranges are reported.

Results

(a) Social interactions

Figure 1 shows the proportion of interactions won by each bird in each aviary. It is clear that in each aviary one male won a considerably greater proportion of interactions than the other birds. This bird was therefore deemed to be dominant over his conspecifics, and was subsequently removed (along with his partner in Aviaries A & B) during the 'dominant removed' condition.

(b) Caching

Throughout the experiment, items were cached more or less exclusively on the aviary floor. The number of caching events that occurred in each aviary during the 'dominant present' condition did not differ significantly between aviaries (Friedman's ANOVA, $\chi_2^2 = 0.4$, $p = 0.81$). Intriguingly, as shown in Figure 2, in each aviary only the dominant bird, and/or his partner, were responsible for the majority, if not all, of the caching events. Indeed, although the dominant male in Aviary A did not cache his partner did, whereas in Aviary B both members of the alpha pair cached, and in Aviary C only the dominant male cached.

The number of items cached during the 'dominant removed' condition was analysed using a Friedman's ANOVA. No significant differences were detected between aviaries (Friedman's ANOVA, $\chi_2^2 = 0.8$, $p = 0.64$). As shown in Figure 3, during the 'dominant removed' condition, the former beta males (now the dominant males) and their partners were now responsible for almost every caching event.

The number of times the beta males cached during each trial in the 'dominant present' and 'dominant removed' conditions was compared statistically. As shown in Figure 4, the beta males cached significantly more items when the dominant bird had been removed from the aviary than when it was present (Aviary A, Wilcoxon's paired test, $z = 2.5$, $N = 10$, $p < 0.01$; Aviary B,

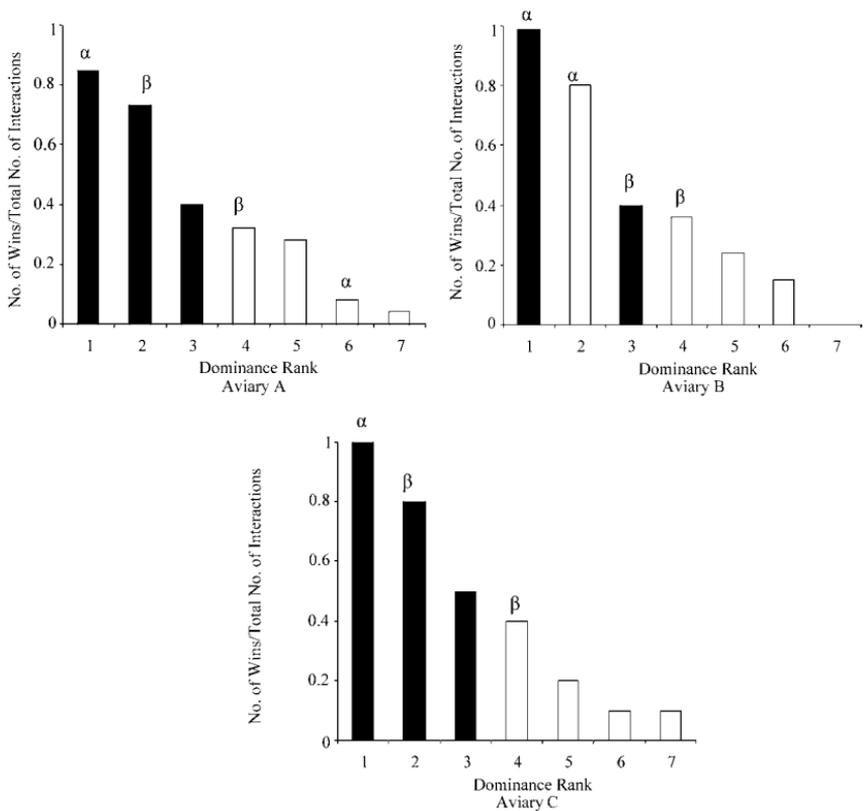


Figure 1. The proportion of interactions won by each bird in each aviary during the ‘dominant present’ condition. The dark bars represent the male birds, and the light bars the females. α indicates the members of the alpha pair, and β the beta pair. Note that the α male in Aviary C did not have a partner.

Wilcoxon’s paired test, $z = 2.5$, $N = 10$, $p < 0.01$; Aviary C, Wilcoxon’s paired test, $z = 1.75$, $N = 10$, $p < 0.01$).

As so few birds cached food items, it was not possible to correlate a bird’s dominance rank with the number of times they cached. It is clear however, that in the ‘dominant present’ condition only the dominant male and/or their partners’ cached, and that in the ‘dominant removed’ condition, the beta male (who is now dominant) and his partner were responsible for the majority of caching events. It was not the case, however, that only the dominant birds accessed the food resource during either condition. Indeed, as shown in Figure 2, during the ‘dominant present’ condition 3 birds from Aviary A, and all 7 birds in Aviaries B & C, ate from the food bowl. As so few birds ate

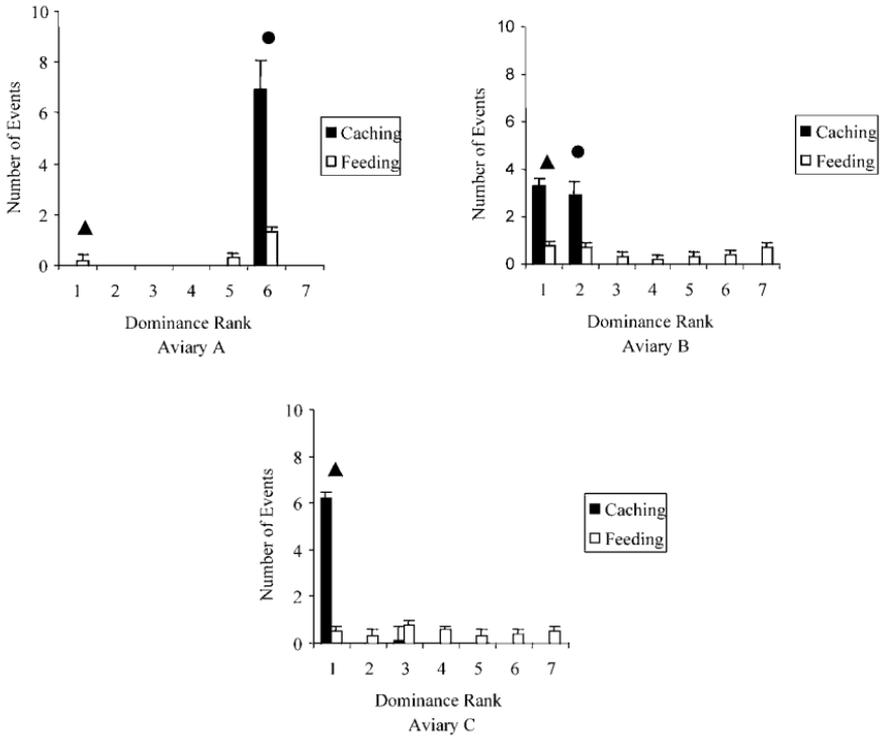


Figure 2. The number of times a bird of each rank either cached or fed during the ‘dominant present’ condition (\pm S.E.M.). ▲ denotes the dominant male, ● denotes the partner of the dominant male (where applicable).

from the food bowl in Aviary A, we were unable to correlate dominance rank and feeding order, however, there were no significant correlations between dominance rank and the order in which the birds fed from the bowl in either Aviary B (Spearman’s Rank, $z = 0.3$, $p = 0.79$), or C (Spearman’s rank, $z = 0.7$, $p = 0.48$). Furthermore, no correlations were detected between a bird’s dominance rank and the number of times they ate from the food bowl during the ‘dominant present’ condition (Aviary A, Spearman’s rank, $z = 0.22$, $p = 0.82$; Aviary B, Spearman’s rank, $z = 1.4$, $p = 0.16$; Aviary C, Spearman’s rank, $z = 0.6$, $p = 0.54$).

Unfortunately, it was not possible to compare statistically the number of items that each bird ate whilst at the food bowl. The tendency for several birds to access the food bowl at the same time, the rapidity with which birds ate, and the fact that the birds often place multiple food items in their pouch,

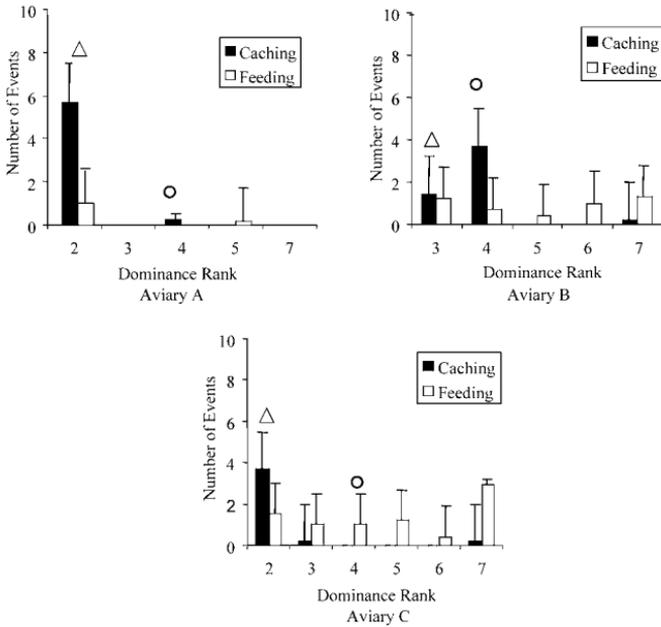


Figure 3. The number of times a bird of each rank either cached or fed during the ‘dominant removed’ condition (\pm S.E.M.). Δ denotes the beta male (now dominant), \circ denotes their partner (where applicable).

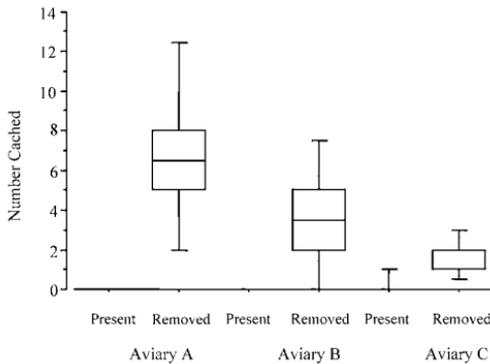


Figure 4. A box and whisker plot showing the median number ($+25^{\text{th}}$ and 75^{th} percentiles) of times the β -males cached in the ‘dominant present’ and ‘dominant removed’ condition.

meant that it was difficult to determine precisely how many items were eaten by each bird at any one time.

Interestingly, storers tolerated their partners recovering and eating their caches, whereas other members of the group were always treated aggress-

sively if they approached a cache site. As such, instances of cache recovery by the storer's partner were not categorised as pilfering attempts. During each trial, storers and their partners often moved caches from one site to another. No significant differences were detected in the number of times the birds moved their own or their partner's caches (dominant pair-male, Wilcoxon's paired test, $z = 0.4$, $N = 10$, $p = 0.65$; -female Wilcoxon's paired test, $z = 1.1$, $N = 10$, $p = 0.26$; sub-dominant pair-male, Wilcoxon's paired test, $z = 1.2$, $N = 10$, $p = 0.22$; -female, Wilcoxon's paired test, $z = 1.6$, $N = 10$, $p = 0.11$).

The total number of times birds moved caches around during a trial was correlated with the number of times conspecifics attempted to pilfer their caches. In Aviary B, significant correlations were detected for both the 'dominant present' (Spearman's rank, $z = 2.7$, $p = 0.05$) and 'dominant removed' conditions (Spearman's rank, $z = 2.6$, $p = 0.01$). In Aviary C, the correlation was significant for the 'dominant removed' condition (Spearman's rank, $z = 2.7$, $p = 0.02$), and a trend identified for the 'dominant present' condition (Spearman's rank, $z = 2.1$, $p = 0.06$). It is noteworthy however, that although this correlation did not reach significance, caches were never moved on those trials where no pilfering attempts were made.

Discussion

There are three key findings from this experiment. First, although a bird's dominance rank does not affect their ability to access and feed from a food resource, only the most dominant male, and/or his partner cache food in the aviary. Second, when the dominant individual and his partner were removed, the second most dominant bird and their partner became the main cachers. Finally, storers often move caches multiple times during a trial, and the number of times they do so increases with the number of times conspecifics attempt to pilfer their caches.

The propensity for dominant birds to cache more items than their subordinate counterparts is an effect that has been identified in mountain chickadees (Pravosudov et al., 2003). Moreover, similarly to the current experiment, Lahti et al. (1998) found that caching in subordinate willow tits increased significantly upon the removal of the dominant bird. There are two possible explanations for the occurrence of suppressed caching rates in subordinates

when in the presence of more dominant individuals. First, at a functional level, that subordinates are sensitive to the increased risk that a dominant observer poses to cache safety, as they would be unable to physically defend their caches from a dominant thief. Thus, in the current experiment, once the dominant jays had been removed, the beta male and his partner began to cache as the main threat to cache safety had been removed. Second, at a causal level, that caching suppression may be analogous to reproductive suppression in some mammal species (marmosets, *Callithrix jacchus*, Abbott et al., 1988; Damaraland mole-rats, *Cryptomys damarensis*, Bennett et al., 1996; yellow-bellied marmots, *Marmota flaviventris*, Oli & Armitage, 2003), and under hormonal control.

Birds respond to increased stress in their social and physical environment by elevating their levels of plasma corticosterone (Wingfield et al., 1997; 1998). For example, Pravosudov et al. (2001) found that, in mountain chickadees (*Poecile gambeli*), corticosterone levels increased in response to limited or unpredictable food availability. Elevated corticosterone levels have been linked to the promotion of increased feeding activity, and to the generation of increased fat stores (Wingfield & Silverin, 1986; Gray et al., 1990; Astheimer et al., 1992), behaviours that, in an impoverished foraging environment, would increase an individual's likelihood of survival. In food-caching birds, experimentally increasing corticosterone levels not only facilitates an increase in feeding activity (Pravosudov et al., 2003), but also results in elevated caching rates (Pravosudov et al., 2003) and in enhanced spatial memory for cache locations (Pravosudov et al., 2003; Saldanha et al., 2000). Contrary to the findings of Pravosudov et al. (2003), however, caching rates in subordinate scrub-jays did not increase in response to competition for access to a depleting food resource, a situation that would appear to represent a stressful event, and might therefore have resulted in an increase in circulating corticosterone. This suggests that the suppression of caching behaviour in subordinate scrub-jays might be the result of a cognitive, rather than a physiological, process. In order to determine whether this was the case, however, it would have been necessary to measure the levels of hormones (e.g., corticosterone) in both dominant and subordinate birds.

Like several other corvids, storing scrub-jays successfully use aggression to drive potential thieves away from cache sites (Eurasian jays, Goodwin, 1986; Bossema, 1979; Wilmore, 1977; rooks, Goodwin, 1986). In this experiment however, aggression appeared to be used in conjunction with another strategy, namely moving caches around (see also Dally et al., in press).

Whilst aggressive defence is an effective cache protection tactic in dominant birds, it is also an energetically expensive and potentially dangerous one. Indeed, injuries sustained during an aggressive interaction can result in fatalities for both combatants, not only the would-be thief. By repeatedly moving items around, however, storsers might reduce the accuracy with which competitors are able to use observational spatial memory to facilitate cache theft, and therefore the need for aggressive cache defence, as memory for the location of prior cache sites might interfere with the memory for current cache location. It is known, however, that moving caches around does not affect the accuracy with which storsers are able to recover their own caches (Dally et al., in press). What is of particular interest in this experiment is that few, if any, caches were moved on those trials when no pilfering attempts took place. Furthermore, the number of times birds moved caches around on each trial increased relative to the number of times conspecifics attempted to steal their caches. Yet this cannot be ascribed to a propensity to move items when a pilferer is approaching. Indeed, items were moved around throughout the caching period, and were aggressively defended, not removed, when a pilferer approached a cache site. This finding suggests that repeated cache movement is not simply an 'automatic' response that is used on the basis of whether or not conspecifics are present. Instead, it appears to be used flexibly depending on the degree of risk posed by observers.

The ability to differentiate between observers that do and do not pose a risk to cache safety represents a clear advantage to storsers. During this study, not all conspecifics were prevented from accessing the storer's cache sites; partners often moved one another's caches. In ravens, there is also observational evidence to suggest that storsers do not use cache protection strategies if their partner is the only witness to a caching event (Heinrich & Pepper, 1998). These findings suggest that, at least in corvids such as ravens (Wilmore, 1977) and scrub-jays (Curry et al., 2002) that form long-term pair bonds, cachers do not appear to perceive their partner as a threat to cache safety.

Our current findings suggest that western scrub-jays adjust their caching strategy as a function of the immediate social environment, and their social relationship with potential thieves. Furthermore, we suggest that, in a social environment, the suppression of caching in subordinate birds is most likely under cognitive, rather than hormonal, control, and that it represents a response to the elevated risk of cache pilferage by dominant conspecifics.

Acknowledgements

This work was supported by grants to NSC from the BBSRC S16565, Marie-Curie, Clare College, and the University of Cambridge. NJE was funded by a Royal Society University Research Fellowship. JMD received financial support from Clare College, the University of Cambridge, the Sir Richard Stapely Educational Trust and the Sefton Educational Trust. We thank Selvino de Kort, Cristoph Teufel & Amanda Seed for comments on an earlier version on the manuscript. These experiments comply with the UK Home Office regulations concerning animal research and welfare, as well as the University of Cambridge regulations on the use of animals.

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