RESEARCH PAPERS

The Effects of Social Context on the Food-Caching Behavior of Florida Scrub-Jays (*Aphelocoma coerulescens*)

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Abstract

Florida scrub-jays are cooperative breeders that live in family groups consisting of a breeding pair, often with several non-breeding helpers. Florida scrub-jays cache food by scatter-hoarding items for later consumption. Within family groups, members have the opportunity to observe and pilfer the caches of other members. We observed jays harvesting experimentally provisioned peanuts alone and in the presence of other family members, to determine whether jays modify their food-handling behavior relative to social context. Non-breeding helpers were less likely to cache in the presence of the dominant male breeder than when alone and all jays tended to cache out of sight when observed by another jay. These changes in caching behavior are consistent with cache protection strategies employed by other species. However, the adaptive value of such cache protection within a sedentary cooperatively breeding family group on a year-round territory is unclear.

Introduction

Food caching is considered adaptive when caching individuals are more likely to retrieve their caches than probable thieves (Andersson & Krebs 1978; but see Smulders 1998; Vander Wall & Jenkins 2003). A number of species employ strategies to avoid cache theft (reviewed in Dally et al. 2006b). Recent studies suggest that western scrub-jays (*Aphelocoma californica*) recognize various social contexts and modify their food-caching behavior to minimize cache theft (Dally et al. 2005a,b, 2006a). These strategies include caching at a distance, caching out of sight, recaching items cached in the presence of an observing jay, or simply feeding on the food item instead of caching (Emery et al. 2004; Dally et al. 2005a,b, 2006a). These strategies appear to be mediated by the dominance relationship between the observing and caching individuals, such that subordinate individuals are less likely to cache and more likely to move cached items when observed by a dominant individual (Dally et al. 2005b, 2006b).

Here we examine the caching behavior of the Florida scrub-jay (*Aphelocoma coerulescens*), a sister species of the western scrub-jay. The habitat specificity and social behavior of Florida scrub-jays differ in several important ways from western scrub-jays. Florida scrub-jays are restricted to xeric oak scrub during the short seral stage (5–20 yr) following fires while western scrub-jays tolerate a broader range of habitats across a much larger geographic range (Woolfenden & Fitzpatrick 1984, 1996; Curry et al. 2002). Florida scrub-jays are cooperative breeders and live in family groups consisting of a breeding pair with zero to several non-breeding helpers on an all-purpose year-round territory that they defend from neighboring jays (Woolfenden & Fitzpatrick 1984, 1996). Florida scrub-jays are remarkably sedentary and family groups may remain in the same territory for many generations (Woolfenden & Fitzpatrick 1984, 1996). Members of family groups are known to pilfer one another's caches and to defend recently made caches (DeGange et al. 1989). Unlike western scrub-jays, the cost of cache loss to

individual Florida scrub-jays may be reduced by the opportunity for reciprocal cache theft and the inclusive fitness of sharing within family groups and Van-der Wall & Jenkins (2003) have suggested that such systems of reciprocal cache theft, even among unrelated individuals, can be evolutionarily stable. The purpose of this study was to determine if and how free-living Florida scrub-jays modify their caching behavior relative to social context.

Methods

Study Site and Species

We conducted our study using the color-banded population of Florida scrub-jays resident at Archbold Biological Station (ABS) (see Woolfenden & Fitzpatrick 1984, 1996 for detailed description of study site and species). Florida scrub-jays have been studied continuously at ABS since 1969 (Woolfenden & Fitzpatrick 1984, 1996) and the sex, age, and breeding status of virtually all jays in the population were known at the time of our study. Florida scrub-jays at ABS readily approach human observers and are accustomed to receiving peanut bits from them. Within Florida scrub-jay family groups a dominance hierarchy exists: males dominate females and within sexes breeders dominate non-breeding helpers (Woolfenden & Fitzpatrick 1977). Male helpers within these family groups also develop dominance hierarchies, often based on their age (Woolfenden & Fitzpatrick 1984).

Social Contexts

We observed breeding and non-breeding jays of both sexes (hereafter referred to as 'social class', i.e. male breeder, male helper, female breeder, or female helper) in a variety of family social contexts, consisting of zero to four additional jays present with the focal jay. We considered additional jays present if we could see or hear them while we followed the focal jay. To explore the effect of social dominance on caching behavior we categorized each trial as one of four social contexts, based on the presence of the most dominant jay: (1) alone: only the focal jay was present, (2) female breeder: anytime the female breeder was present with the focal jay and no males were present, (3) male helper: one or more non-breeding males were present with the focal jay and the breeding male was absent, (4) male breeder: anytime the breeding male was with the focal jay. We did not include the presence of female helpers as

a specific social context because few family groups had non-breeding female members. The sex ratio of helpers is skewed toward males because females tend to disperse earlier and more often from their natal territories in search of breeding opportunities (Woolfenden & Fitzpatrick 1984). Breeding jays were not observed in the presence of other breeding jays because breeders defend territories year-round from neighboring jays and are rarely in the presence of other breeders except during territorial conflicts. Trials in which fledglings were present were excluded from the analysis because the focal jays often fed them the experimental food items complicating the possible food-handling behaviors beyond the scope of our study.

Field Trials

We conducted field trials between 07:30 and 18:15 hours from 5 April 2004 to 23 July 2004 which coincided with the middle to late breeding season for the Florida scrub-jay. We conducted observations opportunistically during the course of other fieldwork and no effort was made to randomize the order that individuals in different social contexts were observed. Trials involving the same focal jay were conducted at least 24 h apart. Before beginning a trial, we identified all jays present by their unique color-band combination. Then, half a peanut in the shell was tossed on the ground 3–5 m away from the observer (MBT). The trial began when the focal jay picked up the peanut. No effort was made to select specific focal individuals and the focal individual was most often the first jay to pick up the peanut. We followed the jay closely (within 5–10 m) and recorded the fate of the peanut (cached or eaten), handling time, distance from start point, and all encounters with other jays. A peanut was considered cached if more than 50% of the edible portion was stored, otherwise we considered it eaten. We noted whether the cache site was clearly visible to us or obscured by vegetation or other objects. When the focal jay was out of view we determined the fate of the peanut by considering the amount of time out of view and listening for the sounds of peanut consumption. In all of our visual observations, peanuts were either cached whole or broken up and eaten. We considered a peanut cached out of view if jays were relatively quiet and returned into view quickly (approx. 5 s). We considered a peanut eaten if jays remained out of view longer (approx. 10–15 s) and we could hear pounding noises as the jay broke the peanut into small pieces with its bill. We assumed

that our ability to see a jay caching was a reasonable proxy for other jays being able to view the cache site because most out-of-view caches were made under dense scrub which was likely to obscure the cache site regardless of the observer's position. Handling time was measured with a stopwatch and defined as the time between when the peanut was picked up until all of the edible parts of the peanut were cached or eaten. We measured the distance, to the nearest meter, from the starting point of the each trial to the location where the peanut was cached or eaten. During trials, the focal jays sometimes had obvious interactions with other jays, such as scramble competition when the peanut was presented or chases once a jay had picked up the peanut. We considered such encounters to have occurred when another jay approached within approx. 30 cm of the focal jay at any time during the trial.

Trials in which the fate of the peanut could not be determined were omitted from the analysis. A total of 194 observations of 131 different focal jays were used in our analyses. Observations of the same jay in different social contexts were treated as independent. Fourteen jays were observed in the same context on different days. The majority of these jays (12/14) cached or ate the peanut as they had in the previous trial and these observations were aggregated and mean values calculated for distance and handling time.

Statistical Analyses

We compared the frequency of caching (vs. eating) the peanut when alone across social class with a Pearson's chi-squared test. We then compared the frequency of caching in each social context with expected frequencies based on the frequency of caching when alone for each social class separately. When mean expected frequencies were less than 6 we calculated log-likelihood ratios rather than chi-squared values (Zar 1999). Some social classes of individuals were not observed in all social contexts and other classes were unlikely to cache in certain contexts. Therefore, we collapsed social context into three categories for subsequent analyses: (1) alone: only the focal jay present, (2) social without encounter: any time other jays were present but no encounters occurred with the caching jay, and (3) social with encounter: anytime an encounter occurred between the caching jay and another jay. We compared the frequency of caching in or out of our view in each social context with expected frequencies based on the frequency of caching in or out of view when alone for all social classes combined in a Pearson's chi-squared test. We used analysis of variance (ANOVA) to determine the effects of social context and class on the distance to cache site and handling time of the cached peanut with social context, class, and the interaction of social context and class as factors. Distance and time data were natural log-transformed to meet the assumptions of parametric statistics.

Results

When alone, jays cached at a similar frequency regardless of social class ($\chi^2 = 1.08$, df = 3, p = 0.781; Fig. 1a–d). The frequency of caching among non-breeding helpers differed significantly in the presence of other jays when compared with caching alone (male helper: G = 13.48, df = 2, p = 0.001, Fig. 1a; female helper: G = 7.23, df = 2, p = 0.027, Fig. 1b). Male and female helpers rarely cached in the presence of the male breeder and male helpers cached less often in all social contexts than when alone (Fig. 1a,b). Contrary to our expectations, female helpers cached frequently in the presence of the female breeder and male helpers. Breeders cached at similar rates across all social contexts (male: $\chi^2 = 0.18$, df = 2, $P = 0.673$, Fig. 1c; female: $\chi^2 = 0.57$, df = 2, p = 0.450, Fig. 1d). The number of addition jays present (1–4) did not appear to influence the likelihood of caching for any social class of focal jays ($\chi^2 \leq 3.841$, df = 3, p $\geq$ 0.279). The behavior of the other jays did not appear to influence the decision to cache; focal jays cached with the same frequency whether or not an encounter occurred with another jay ($\chi^2 = 0.828$, df = 1, p = 0.363). Focal jays cached in 24 of 53 trials when jays were present but no encounters occurred and cached in 26 of 70 trials when an encounter occurred with another jay.

Jays were more likely to cache out of our view when observed by other jays than when alone ($\chi^2 = 10.47$, df = 2, p = 0.001; Fig. 2). The distance from the start point of each trial to the final cache location tended to be greater in trials where encounters occurred with other jays (Fig. 3); however this trend was not statistically significant ($F_{2,70} = 1.77$, p = 0.279). The social class of the focal jay had no significant effect on the distance to the cache site ($F_{3,70} = 2.33$, p = 0.338). Distance to cache site averaged 25.3 ± 2.7 m (± SE) among male breeders; 32.4 ± 4.3 m among female breeders, 37.6 ± 7.9 m among male helpers, and 18.7 ± 4.6 m among female helpers. Social class significantly influenced
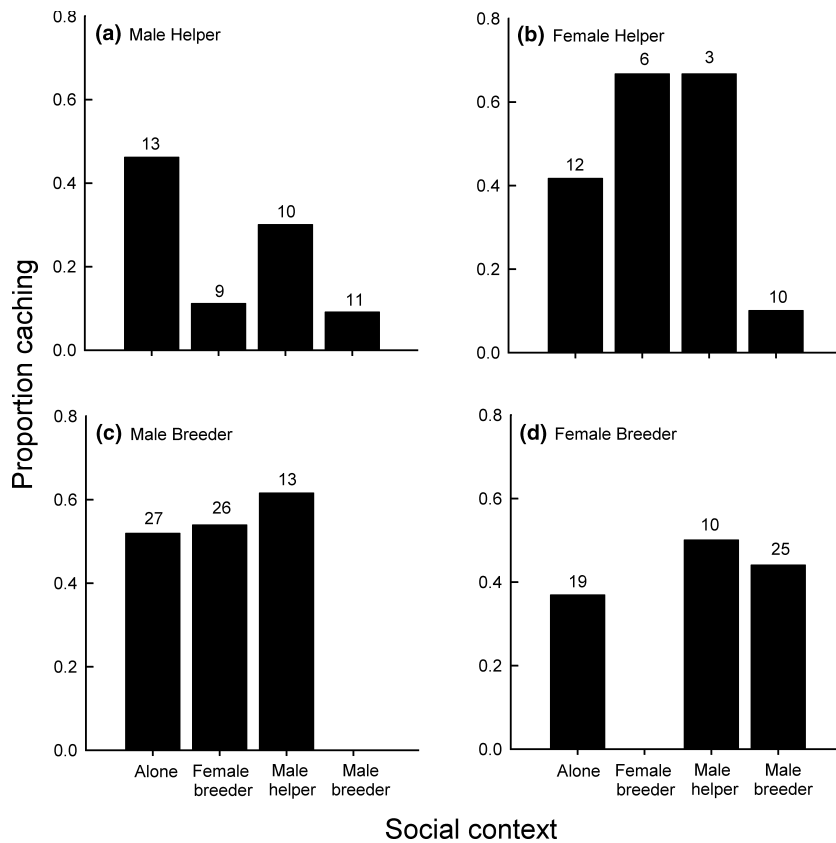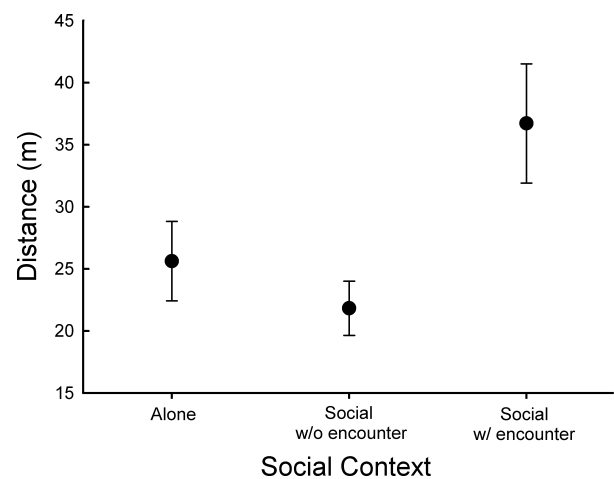
Fig. 1: The proportion of observations in which the (a) male helper, (b) female helper, (c) male breeder, and (d) female breeder cached an experimentally provisioned peanut in each of four social contexts. Breeders were never observed with breeders of the same sex (see text) and the total number of observations is given above each bar. The proportion of caches made in social contexts differed significantly from the number of caches made when alone for male and female helpers (p < 0.03)
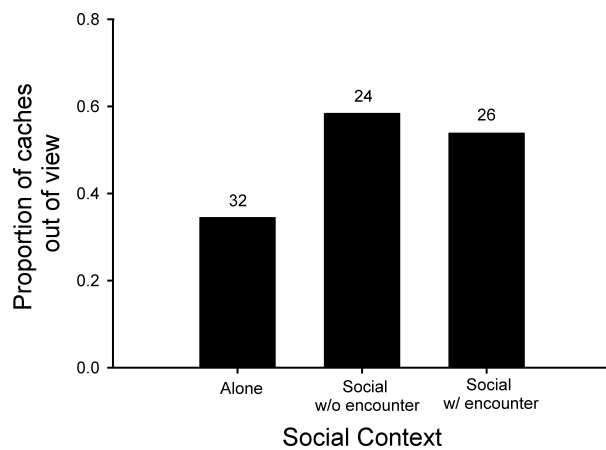
Fig. 2: The proportion of caches made out of view of the researcher in each of three social contexts. Significantly more caches were made out of view when observing jays were present (p = 0.001)

Fig. 3: The mean (±SE) distance from the location where the peanut was picked up by the jay to the cache site for each of three social contexts. Despite an apparent trend no significant difference existed among social contexts (p = 0.279)

the amount of time the focal jay handled the peanut before caching ($F_{3,70}$ = 3.61, p = 0.020). Handling time for male breeders averaged 70.1 ± 6.3 s, female breeders 117.4 ± 21.2 s, male helpers 116.7 ± 22.0 s, and female helpers 107.7 ± 17.7 s; however, none of the pairwise comparisons of handling time

among sex and breeding status were significantly different (Bonferroni post hoc test p > 0.126). Handling time did not differ significantly with social context ($F_{2,70}$ = 0.17, p = 0.796) but a trend existed for

increased handling times when encounters occurred with other jays. Handling time averaged 89.5 ± 10.3 s when alone, 79.7 ± 9.7 s when other jays were present but no encounters occurred, and 116.2 ± 19.1 s when encounters occurred with other jays.

Discussion

Our observations suggest that Florida scrub-jays respond to social context when making food-caching decisions. Subordinant non-breeding helpers rarely cached in the presence of the dominant male breeder; similar to the findings of Dally et al. (2005b) for western scrub-jays. Dally et al. (2005b) found that members of the dominant breeding pair were more likely to cache in social contexts than subordinate helpers, who tended to feed on food items rather than caching. They suggested that eating a food item rather than caching it in the presence of socially dominant birds may be a strategy to avoid the loss of food by cache theft (Dally et al. 2005b). Carrascal & Moreno (1993) attributed a decline in the caching rate of nuthatches (*Sitta europaea*) in the presence of conspecifics to the perceived threat of cache loss. Similar changes in caching frequency have been observed in black-capped chickadees (*Poecile atricapilla*) (Stone & Baker 1989) and willow tits (*P. montanus*) (Lahti & Rytkönen 1996). Brunell & Tomback (1985) found that gray jays (*Perisoreus canadensis*) would not cache in the presence of a Steller's jay (*Cyanocitta stelleri*), a known cache thief, and suggested that gray jays recognized Steller's jays as thieves and changed their behavior to limit cache theft. In our study the suppression of caching was most pronounced among non-breeding helpers in the presence of the male breeder. Within family groups, the male breeder dominates all non-breeding jays (Woolfenden & Fitzpatrick 1977) and helpers may perceive the male breeder as an immediate threat to their caches. The dominance of the male breeder may allow it to defend its caches against immediate theft by all other jays and to pilfer the caches of subordinate jays. Consistent with this explanation, we found that the male breeder cached at similar rates regardless of social context or encounters with other jays.

Social dominance appears to play an important role in the caching behavior of Florida scrub-jays in social contexts however; we observed several incidences in which subordinates cached frequently despite the presence of dominant jays. Female breeders are subordinate to the male breeder and male helpers (Woolfenden & Fitzpatrick 1977), but we found that they cached at similar rates regardless of social context. It seems unlikely that male breeders pilfer the caches of their mates because food sharing is an important part of pair bond development and maintenance and male to female courtship feeding is common (Woolfenden & Fitzpatrick 1996). In general, aggressive dominance interactions between members of the breeding pair are rare (Woolfenden & Fitzpatrick 1977). In western scrub-jays, Dally et al. (2005b) observed that members of the dominant pair frequently cached in one another's presence and tolerated the recovery of their caches by the other member. The pair bond may also mediate interactions between the female breeder and male helpers. Male helpers are clearly dominated by the male breeder and the male breeder has been observed to intervene in interactions between the female breeder and other jays, driving them away from its mate (Woolfenden & Fitzpatrick 1984). Such interventions, where they occur during foraging, could provide a degree of cache protection for the female breeder. These interactions especially may be important during the breeding season, when our observations occurred. Female helpers are subordinate to all other social classes of jays (Woolfenden & Fitzpatrick 1977), but cached frequently in the presence of the female breeder and male helpers. This pattern differs from our expectations and we have no clear explanations why this might occur. However, we observed relatively few female helpers in the presence of male helpers (n = 3) and half of our observations (3/6) of female helpers with the female breeder were members of the same family group. Therefore, the inferences we can make from these data are limited.

When caching did occur, our results suggest that Florida scrub-jays may use behavioral tactics to avoid cache theft. In the presence of other jays, caches were made out of view more often than when alone; thus, it appears that Florida scrub-jays avoid observation when caching. Caching out of view has been described as a protection strategy employed by both western scrub-jays (Dally et al. 2005a) and common ravens (*Corax corax*) (Bugnyar & Kotrschal 2002). We found a non-significant trend toward caching at greater distance when encounters occurred with other jays, a behavior that is consistent with cache protection strategies in gray jays (Waite 1992), willow tits (Lahti et al. 1998), and western scrub-jays (Dally et al. 2005a). However, our measure represents only the distance from the beginning of an observation to the final cache site

and does not take into account the actual distance between observing and caching jays when the cache was made. In many cases, the observing jay may have followed the caching jay. Consistent with these changes in caching behavior, we also observed non-significant trends increased handling time prior to caching when encounters occurred. It is important to note that because of sampling limitations, these observations of caching location and distance were pooled across social contexts with different dominance patterns that are known to mediate caching behavior (Dally et al. 2005a, 2006b). Our presence as human observers also may have affected caching behavior; common ravens are capable of recognizing and following the gaze of human observers (Bugnyar et al. 2004).

Common ravens, western scrub-jays, and Eurasian jays (*Garrulus glandarius*) are known to move and re-cache food if they have been observed by conspecifics when making their initial caches (reviewed in Dally et al. 2006a). It is possible that breeding Florida scrub-jays employ this strategy in addition to modifying their immediate caching behavior. However, the observations we present here cannot address this possibility because we did not monitor the caches after they were made. In a separate study of acorn cache recovery, I. Kulachi, R. Bowman & Woolfenden (unpubl. data) found no significant differences among social classes in the likelihood of recovered caches (of unknown origin) being eaten or recached.

On a proximate level, the context-dependent caching behavior of Florida scrub-jays can be interpreted as a strategy to avoid the loss of food to conspecifics, consistent with observations in other species (reviewed in Dally et al. 2005a). However, the ultimate explanation for cache protection in the Florida scrub-jay is much less clear. Florida scrub-jays individually cache many more acorns than they recover to eat (DeGange et al. 1989) and also feed on generally abundant arthropods and small vertebrates, suggesting that loss of a few acorns to cache theft might be unimportant. The cost of cache loss is reduced further by the opportunity for reciprocal cache theft and the inclusive fitness of sharing with family members (Vander Wall & Jenkins 2003). However, food availability varies and can be reduced dramatically under certain environmental conditions, during which predictable access to cached food could be important. Florida scrub-jays are closely related to western scrub-jays, share many behavioral and morphological characteristics, and have only recently been recognized as a separate species

(American Ornithologists' Union 1995). Cache protection behavior in the Florida scrub-jay may be a phylogenetic vestige of past social and ecological conditions of the scrub-jay.

Acknowledgements

Literature Cited

American Ornithologists' Union. 1995: Fortieth supplement to the American Ornithologists' Union Check-list of North American birds. Auk **112**, 819—830.

Andersson, M. & Krebs, J. 1978: On the evolution of hoarding behaviour. Anim. Behav. **26**, 707—711.

Brunell, K. L. & Tomback, D. F. 1985: Steller's jays steal gray jay caches: field and laboratory observations. Auk **102**, 417—419.

Bugnyar, T. & Kotrschal, K. 2002: Observation learning and the raiding of food caches in ravens, *Corvus corax*: is it 'tactical' deception? Anim. Behav. **64**, 185—195.

Bugnyar, T., Stowe, M. & Heinrich, B. 2004: Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. Proc. R. Soc. Lond. B Biol. Sci. **271**, 1331—1336.

Carrascal, L. M. & Moreno, E. 1993: Food caching versus immediate consumption in the nuthatch: the effect of social context. Ardea **81**, 135—141.

Curry, R. L., Peterson, A. T. & Langen, T. A. 2002: Western scrub-jay (*Aphelocoma californica*). In: The Birds of North America (Poole, A. & Gill, F., eds). The Academy of Natural Sciences, Philadelphia, PA; The American Ornithologists' Union, Washington, DC, No. 712.

Dally, J. M., Emery, N. J. & Clayton, N. S. 2005a: Cache protection strategies by western scrub-jays, *Aphelocoma californica*: implications for social cognition. Anim. Behav. **70**, 1251—1263.

Dally, J. M., Emery, N. J. & Clayton, N. S. 2005b: The social suppression of caching in western scrub-jays (*Aphelocoma californica*). Behaviour **142**, 961—977.

Dally, J. M., Clayton, N. S. & Emery, N. J. 2006a: The behavior and evolution of cache protection and pilferage. Anim. Behav. **72**, 13—23.

Dally, J. M., Emery, N. J. & Clayton, N. S. 2006b: Food-caching western scrub-jays keep track of who was watching when. Science **312**, 1662—1665

DeGange, A. R., Fitzpatrick, J. W., Layne, J. N. & Woolfenden, G. E. 1989: Acorn harvesting by Florida scrub-jays. Ecology **70**, 348—356.

Emery, N. J., Dally, J. M. & Clayton, N. S. 2004: Western scrub-jays (*Aphelocoma californica*) use cognitive strategies to protect their caches from thieving conspecifics. Anim. Cogn. **7**, 37—43.

Lahti, K. & Rytkönen, S. 1996: Presence of conspecifics, time of day age affect willow tit food hoarding. Anim. Behav. **52**, 631—636.

Lahti, K., Koivula, K., Rytkönen, S., Mustonen, T., Welling, P., Pravosudov, V. V. & Orell, M. 1998: Social influences on food caching in willow tits: A field experiment. Behav. Ecol. **9**, 122—129.

Smulders, T. V. 1998: A game theoretical model of the evolution of food hoarding: applications to the paridae. Am. Nat. **151**, 356—366.

Stone, E. R. & Baker, M. C. 1989: The effects of conspecifics on food caching by black-capped chickadees. Condor **91**, 886—890.

Vander Wall, S. B. & Jenkins, S. H. 2003: Reciprocal pilferage and the evolution of food-hoarding behavior. Behav. Ecol. **14**, 656—667.

Waite, T. A. 1992: Social hoarding and a load size-distance relationship in gray jays. Condor **94**, 995—998.

Woolfenden, G. E. & Fitzpatrick, J. W. 1977: Dominance in the Florida scrub-jay. Condor **79**, 1—12.

Woolfenden, G. E. & Fitzpatrick, J. W. 1984: The Florida Scrub-Jay: Demography of a Cooperative-breeding Bird. Princeton Univ. Press, Princeton, NJ.

Woolfenden, G. E. & Fitzpatrick, J. W. 1996: Florida scrub-jay (*Aphelocoma coerulescens*). In: The Birds of North America (Poole, A. & Gill, F., eds). The Academy of Natural Sciences, Philadelphia, PA; The American Ornithologists' Union, Washington, DC, No. 228.

Zar, J. H. 1999: Biostatistical Analysis, 4th edn. Prentice Hall, Upper Saddle River, NJ.