

# A Game Theoretical Model of the Evolution of Food Hoarding: Applications to the Paridae

Tom V. Smulders

Department of Psychology, Cornell University, Ithaca, New York 14853

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**abstract:** A game against the field is proposed that models the evolution of food-hoarding behavior in a group-living species, like many members of the family Paridae (Aves, Passeriformes). The model predicts that no special retrieval mechanisms (e.g., memory) are necessary for food-hoarding individuals to invade a population of nonhoarders, as long as the winters are very severe. Once food hoarding is established in a population, having smaller groups and separating foraging niches between group members prevent cheaters from benefiting from other individuals' caches. A scenario is proposed for the evolution of hoarding in the Paridae.

**Keywords:** Paridae, game theory, evolution, food hoarding.

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Over the last 20 yr, the study of food hoarding in birds (and recently mammals as well; Jacobs and Spencer 1994) has grown into a multidisciplinary field, encompassing behavioral ecology (Källander and Smith 1990), psychology (Shettleworth 1995), and neurobiology (Sherry et al. 1989; Clayton and Krebs 1995; Smulders et al. 1995). This expansion was initiated by a model exploring the conditions under which food-hoarding behavior would be advantageous and establish itself as a strategy in a population (Andersson and Krebs 1978). The main conclusion that the authors drew in the latter paper is that any hoarding animal must have an advantage over nonhoarding individuals in its group in retrieving the items it has hoarded. If not, the nonhoarding animals would have the same benefits from the hoarded food, without the costs of hoarding, and therefore would outcompete the hoarding animal.

This prediction motivated several researchers to investigate the retrieval mechanisms of different species of

food-hoarding animals. Of these, the families of the Corvidae (crows and jays) and the Paridae (chickadees and titmice) have been most thoroughly studied (e.g., Balda and Kamil 1989; Sherry 1989). A set of laboratory and field experiments suggested that these birds can, and will, use memory for the specific location of a hoard to retrieve that hoard (Balda 1980; Sherry et al. 1981). The precision, duration, and apparent capacity of this memory indicated that this memory might be adaptively specialized (Krebs 1990). This notion was reinforced by neuroanatomical work, which showed that the brain areas involved in this memory (the hippocampal formation) are larger in food-hoarding species than in (related) nonhoarders (Krebs et al. 1989; Sherry et al. 1989). Another retrieval mechanism that has been described is the separation of both caching and foraging niches between individuals, so only the individual who hoarded the food will retrieve it (Brodin 1994*b*). Both retrieval mechanisms will be discussed in this article. Andersson and Krebs (1978) made predictions that were very general and were meant to apply to all group-living animals. However, many parid species live in a very structured social system of winter flocks made up of unrelated individuals (Ekman 1989; Matthysen 1990), which could possibly influence the validity of the predictions. In this article, I propose a mathematical model that is based on a parid-like social organization and examines the circumstances under which food-hoarding behavior could evolve in such a population.

## The Models

### *The Simple Case*

Assume the population size to be large relative to flock size. The individuals live in the same general area and niche throughout the year. After the breeding season, the adults stay on the territory, while their offspring disperse to form winter flocks with unrelated adults and other juveniles several territories away. Winter flock home ranges are larger than breeding territories and are defended

\*E-mail: tvs1@cornell.edu.

against other winter flocks. To simplify the model, we assume that there are two distinct phases to the nonbreeding season: fall, during which food is abundant and excess food can be hoarded, and winter, during which hoarded food can be retrieved. Hoarding food in the fall does not significantly decrease the amount available for immediate consumption because of the vast food abundance. Hoarded food does add to the natural food availability ( $f$ ) during winter. This corresponds to the “long-term hoards” of Brodin and Clark’s (1997) model. Food items are not all hoarded in one location but, rather, are scattered all over the foraging niche. This niche does not change from fall to winter, so the individuals will encounter the caches in the course of normal foraging. In the next breeding season, winter flocks split up again, and the surviving pairs of unrelated birds will occupy breeding territories together. This pattern is based on the winter organization of many parid species (Ekman 1989; Matthysen 1990).

Winter flocks are made up of  $n$  individuals. These individuals survive from fall to winter with probability  $p_s$ . A food-hoarding individual stores  $h$  items in the fall. A fraction  $d$  of these items will remain available until winter. At the time of retrieval, the probability that an individual will recognize and retrieve any single one of these items is  $r$ . For the purpose of this article, the absolute amounts of naturally available and hoarded food are less important than the ratio between them. This means we assume that we are dealing with a total amount of food between the minimum necessary for survival and the maximum an individual could possibly use in one winter. Hoards are scattered all over the home range, so retrieval is not trivial. We assume that hoarding individuals have no advantage in finding and retrieving their own hoards over their flock mates, so  $r$  is independent of the individual retrieving the hoard. This assumption is crucial to investigate whether hoarding could evolve without specialized retrieval mechanisms, like specific memory for the hoarded item’s location. Hoarding items in the fall is assumed to be costly, which is expressed as an increased probability of not surviving from fall to winter ( $p_c$ ). Table 1 summarizes the parameters used in the model. All calculations were done with the help of Mathematica (Wolfram Research 1990) on an Apple Macintosh IIfx.

The fitness of an individual is assumed to be directly related to the amount of food available to that individual, multiplied by the probability that that individual will actually survive from fall to winter. This larger food supply then allows the animal to survive to the breeding season and to start the breeding season in good condition. Only that aspect of fitness that relies on a good food supply in winter is modeled here. The fitness of a nonhoarding individual in a flock of other nonhoarding individuals can

**Table 1:** Parameters of the simple model and their boundaries

Parameter	Definition
$0 \leq f$	The amount of food available to a flock in winter, without hoarding
$0 \leq h$	The amount of food one individual hoards in the fall
$0 \leq d \leq 1$	The fraction of hoarded food that survives from fall to winter
$0 \leq r \leq 1$	The probability that a hoarded food item will be recognized and retrieved
$1 \leq n$	Number of individuals in the flock in the fall
$0 \leq p_s \leq 1$	The probability of surviving from fall to winter
$0 \leq p_c \leq 1$	The cost of hoarding, represented as the extra probability of dying between fall and winter

then be represented as the total amount of food ( $f$ ) available to the flock, divided by the number of individuals still in the flock in winter, and multiplied by the probability that the focal bird itself will still be alive at that point ( $p_s$ ). The mean payoff is (app. A):

$$F_{\text{nn}} = fp_s \left\{ \frac{1}{np_s} [1 - (1 - p_s)^n] \right\}. \quad (1)$$

The fitness of a hoarding individual in a flock of nonhoarding individuals would then be:

$$F_{\text{hn}} = (f + hdr) p_s (1 - p_c) \left\{ \frac{1}{np_s} [1 - (1 - p_s)^n] \right\}. \quad (2)$$

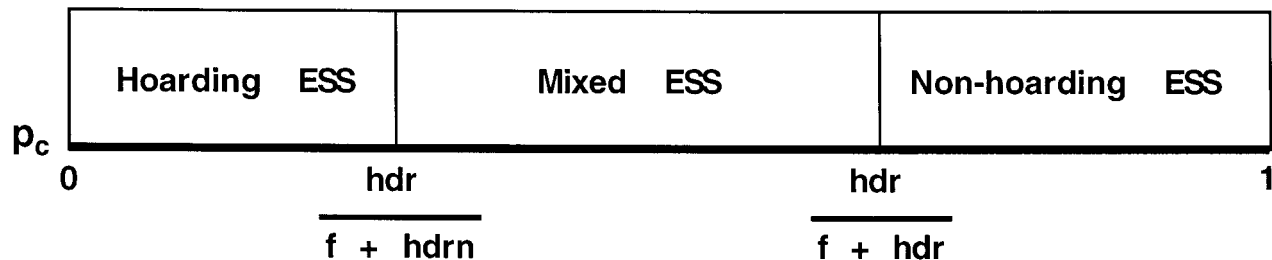
Using the same reasoning, the fitness of a hoarding bird in a flock of hoarding individuals can be described as:

$$F_{\text{hh}} = (f + nhdr) p_s (1 - p_c) \times \left( \frac{1}{np_s(1 - p_c)} \{1 - [1 - p_s(1 - p_c)]^n\} \right). \quad (3)$$

And the fitness of a nonhoarding individual in a flock of hoarding individuals as:

$$F_{\text{nh}} = (f + (n - 1) hdr) p_s \times \left( \frac{1}{np_s(1 - p_c)} \{1 - [1 - p_s(1 - p_c)]^n\} \right). \quad (4)$$

The model is an evolutionary game against the field (Maynard Smith 1982). In this situation, one compares the fitness of the individual playing the new, invading strategy against the average fitness of all the individuals playing the predominant strategy. The population is large, so the influence of the invading strategy is negligible in calculating the average fitness of the resident strategy. In other words, the change in fitness experienced by



**Figure 1:** Solution of the simple case model for  $p_c$ . As  $p_c$  varies from 0 (no cost of hoarding) to 1 (lethal cost), it takes on two boundary values. The lower value is the boundary below which hoarding will be an ESS, the upper value is the boundary above which hoarding cannot invade a population of nonhoarders. Note that the boundaries are functions of  $h$ ,  $d$ ,  $r$ ,  $f$ , and  $n$ .

the individuals in the flock to which the invading, mutant individual belongs is diluted when the fitness of the nonmutant strategy is averaged over all flocks. It therefore follows that an animal playing a food-hoarding strategy will invade a population of animals playing the nonhoarding strategy if

$$F_{hn} > F_{nn}, \tag{5}$$

and a nonhoarding individual will invade a population of hoarding individuals if

$$F_{nh} > F_{hh}. \tag{6}$$

Solving inequalities (5) and (6) for  $p_c$  (i.e., the cost of hoarding; app. B), we find two threshold values for  $p_c$ . Figure 1 shows  $p_c$  varying from 0 (no cost) to 1 (certain death). For the lower values of  $p_c$ , nonhoarders cannot invade a population of hoarding individuals, and the hoarding strategy is an evolutionarily stable strategy (ESS; Maynard Smith and Price 1973). For the values of  $p_c$  between the two threshold values, both the hoarding and nonhoarding strategies could invade each other, and we expect a mixed population or a population of individuals playing mixed strategies. For the higher values of  $p_c$ , the cost of hoarding is too high for hoarders to invade a population of nonhoarders, and nonhoarding is an ESS.

Figure 2 explores the influence of varying  $(hdr)/f$  and  $n$  on the locations of the two boundaries. It is clear that flock size has no influence on the top boundary, below which hoarders can invade, but it does influence how sensitive a population of hoarders is to invading nonhoarders or “cheaters.” Smaller flock sizes make it harder for a cheater strategy to be established. For a high ratio of hoarded food to naturally available food, food hoarders can establish themselves in the population very easily, even when the cost of hoarding is very high. As the ratio decreases, the threshold decreases rapidly as well. A high ratio of hoarded food to naturally available food will also help keep cheaters out of a population of hoarders, as long as the flock size is rather small.

### Niche Separation

In the previous section, we assumed that all individuals are hoarding and foraging in exactly the same niche. Several researchers have shown, however, that even within flocks there is often a slight separation of those niches between the individuals making up the flock (Brodin 1994b; Lens et al. 1994). This niche separation is now included in the model as the following factor:

$q$  = the proportion of the flock niche used by one individual.

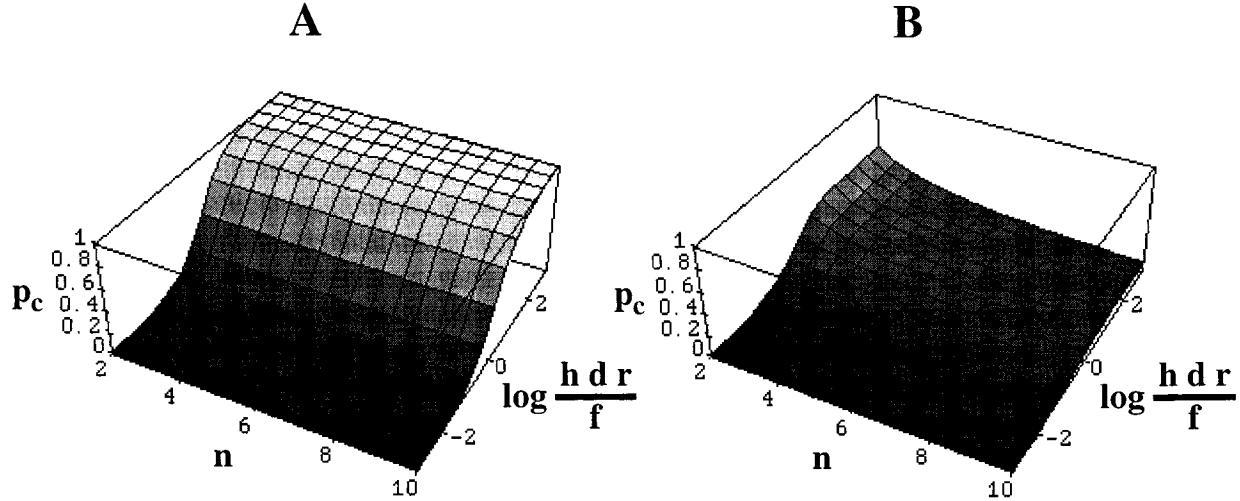
This factor will vary from  $1/n$  (every individual has a completely exclusive hoarding and foraging niche on which its flock mates do not encroach) to 1 (all birds use the same niche; this takes us back to the previous model). As  $q$  decreases, the niches will be more separated between flock members. In the equations, the food supply available to one individual can then be split up into the proportion available exclusively to the focal individual and the proportion it shares with all other individuals ( $\alpha$ ). The total niche space can then be split up into two parts: the exclusive parts, multiplied by the number of flock members, and the part in which all forage together. Formally, this becomes

$$1 = nq(1 - \alpha) + \alpha q \Leftrightarrow \alpha = \frac{nq - 1}{q(n - 1)}. \tag{7}$$

With this modification, the fitness equations become

$$F_{nn} = fp_s \left\{ \frac{1}{np_s} [1 - (1 - p_s)^n] \right\}; \tag{8}$$

$$F_{hn} = \left( f + hdr \frac{qn - 1}{q(n - 1)} \left\{ \frac{1}{np_s} [1 - (1 - p_s)^n] \right\} + hdr \left[ 1 - \frac{qn - 1}{q(n - 1)} \right] \right) p_s (1 - p_c); \tag{9}$$



**Figure 2:** Solution of the simple case model plotted in function of relevant parameters. On the vertical axis, the cost of hoarding ( $p_c$ ) is represented, plotted against the flock size ( $n$ ) and the ratio of hoarded to naturally available food ( $[hdr]/f$ ). Note that the ratio is represented on a logarithmic scale. *A*, Upper boundary below which a hoarding individual can invade a nonhoarding population. *B*, Lower boundary below which hoarding is an ESS.

$$F_{hh} = \left( f + hdn \frac{qn - 1}{q(n - 1)} \right) \times \left\{ \frac{1}{np_s(1 - p_c)} [1 - (1 - p_s(1 - p_c))^n] \right\} + hdn \left[ 1 - \frac{qn - 1}{q(n - 1)} \right] p_s(1 - p_c); \quad (10)$$

and

$$F_{hh} = \left( f + hdn(n - 1) \frac{qn - 1}{q(n - 1)} \right) \times \left\{ \frac{1}{np_s(1 - p_c)} [1 - (1 - p_s(1 - p_c))^n] \right\} p_s. \quad (11)$$

To investigate the effect of increasing niche separation (decreasing  $q$ ) on the invasion boundaries, I calculated the partial derivative to  $q$  of the ratio between the fitness of the invading strategy and the resident strategy (app. C). This yields the following results:

$$\frac{\partial \left( \frac{F_{hh}}{F_{nn}} \right)}{\partial q} \leq 0, \quad (12)$$

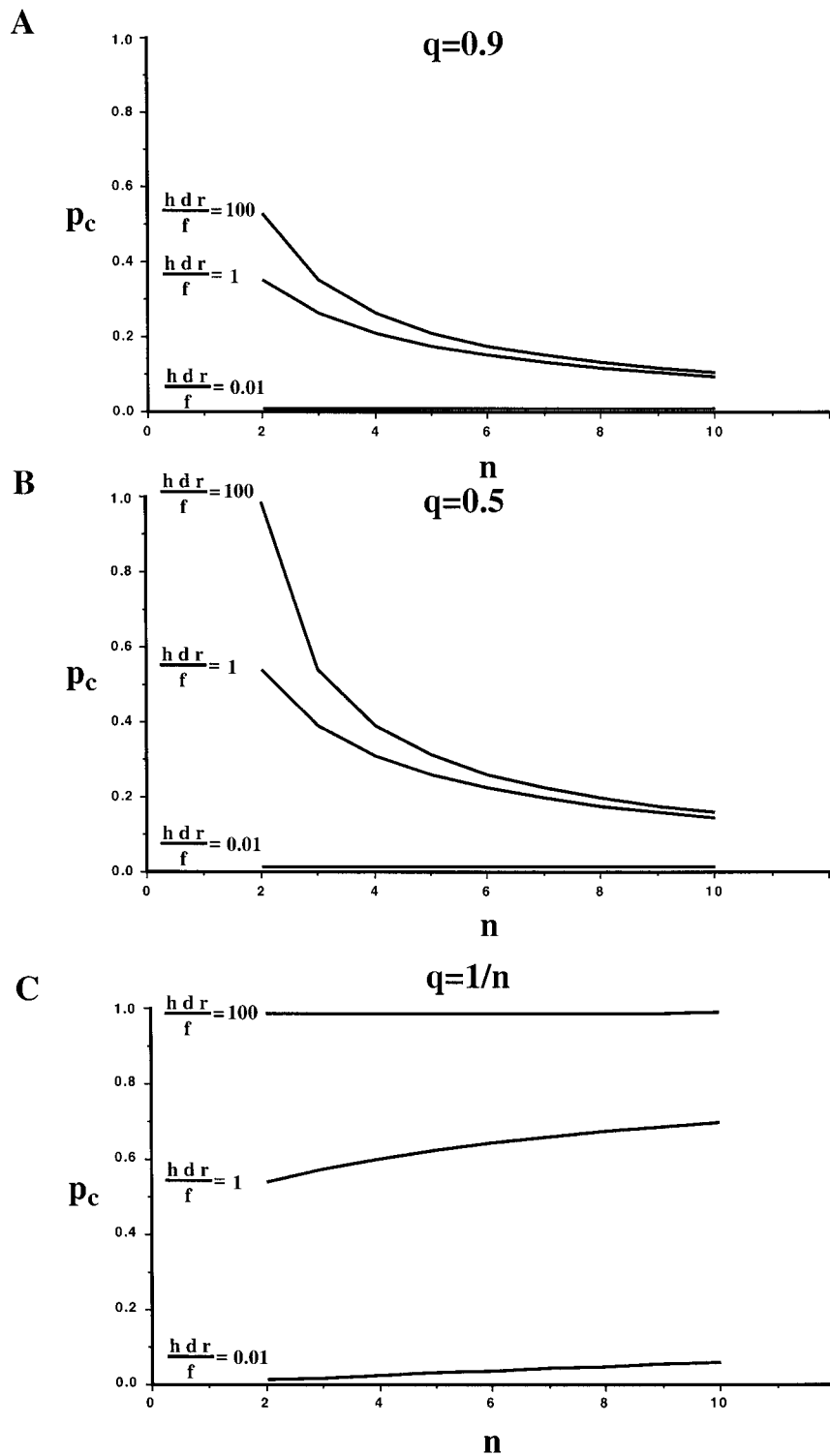
and

$$\frac{\partial \left( \frac{F_{nh}}{F_{hh}} \right)}{\partial q} \geq 0. \quad (13)$$

Expression (12) means that as  $q$  decreases (niches more separated),  $F_{hh}/F_{nn}$  increases or the fitness of the invading hoarding strategy increases relative to the fitness of the resident nonhoarding population. Similarly, expression (13) states that, with increasing niche separation, invading nonhoarders will do less well relative to the resident hoarding population. Figure 3 shows how the invasion threshold for cheaters in a population of hoarders increases with increasing niche separation. To summarize, increasing niche separation increases both invasion ability and stability of the hoarding strategy. This makes intuitive sense because increased niche separation means that nonhoarders have less access to hoarded food, decreasing their success relative to hoarders.

### Discussion

Andersson and Krebs's (1978) main conclusion was that, in a social group, the hoarding strategy could only be adaptive if the hoarding individual was more likely to retrieve its caches than any other group member. This statement has always been interpreted as requiring a specialized retrieval mechanism (memory, niche separation, mnemonic rules, individual preferences, and so on; Shettleworth and Krebs 1982) for hoarding individuals to gain this advantage over possible "cheating" conspecifics. However, it is difficult to imagine how some of these specialized retrieval mechanisms could have been available before the onset of the evolution of hoarding itself in this group. This is especially the case for memory that lasts long enough for it to be useful for retrieval in win-



**Figure 3:** Solution of the niche separation case model plotted in function of relevant parameters. On the vertical axis, the cost of hoarding ( $p_c$ ) is represented, plotted against the flock size ( $n$ ), for different ratios of hoarded to naturally available food ( $[hdr]/f$ ). The normal probability of survival from fall to winter ( $p_s$ ) was found not to have a relevant influence on the model and was arbitrarily set at 0.7. The graphs represent the lower boundary below which hoarding is an ESS. As niche separation increases, the boundary goes up. *A*, The value  $q = 0.9$  represents a large niche overlap between flock members. *B*, For  $q = 0.5$ , flocks of  $n = 2$  are completely separated, while larger flocks have increasing overlaps. *C*, The value  $q = 1/n$  represents total niche separation for all flock sizes.

ter. The present model shows that it is enough that the hoarding individual has an advantage over the average nonhoarding individual across the population, without any special retrieval mechanisms. That the nonhoarding flock mates of the hoarder are even better off than the hoarder itself does not prevent the evolution of food hoarding in the population, as long as the average nonhoarder is worse off. This in no way contradicts Andersson and Krebs's (1978) findings. They concluded that food hoarding could only evolve if it entailed a net benefit for the food-hoarding individual. The current model shows that gaining a net benefit does not require any specialized retrieval behavior on the part of the food hoarder. Andersson and Krebs saw this possibility, as is evidenced by the following quote (1978, p. 708): "Hoarders can also be retained in the population at a low proportion because their 'global' fitness (Matessi and Jayakar 1976), averaged over the population, may be higher than that of non-hoarders." Subsequent discussions of this prediction in the literature have stressed the need for specialized retrieval mechanisms and have ignored the possibility I propose in this model. In addition, the current model predicts that the proportion of hoarders to nonhoarders can be more than low (up to a complete population of hoarding individuals), given the right ecological circumstances.

Food-hoarding species have a good memory for stored food (e.g., Hitchcock and Sherry 1990) and have an enlarged hippocampus, which is involved in this memory (Krebs et al. 1989; Sherry and Vaccarino 1989; Sherry et al. 1989). How does the existence of this memory ability affect the model? For memory to be useful in retrieval in the model (i.e., increase  $r$ ), it would have to be fairly long-term (from fall to winter). The maximum estimate of memory for caches in parid species is only 4–6 wk (Hitchcock and Sherry 1990; Brodin 1994a). This indicates that memory for item location may not be used to increase  $r$ , at least not in the time frame addressed by this model. Brodin and Clark (1997) suggest that memory is only used for short-term retrieval as an alternative to fat reserves. This possibility is not addressed in the present model and is not mutually exclusive with it. Their model postulates the same mechanism for long-term retrieval as presented in the present model and comes to the conclusion that selection for long-term, large capacity memory would be weak at best. Memory could also be advantageous during hoarding rather than retrieval (Smulders and Dhondt 1997). Individuals want to distribute their caches as evenly as possible over their niche to avoid kleptoparasitism (Sherry et al. 1982). Remembering where other items have been hoarded allows them to do this efficiently. This in effect increases  $d$  (the fraction of hoards still present in winter). In addition, memory can

lower the cost of hoarding ( $p_c$ ). This cost is threefold: any time spent hoarding cannot be spent on other activities; flying to and from the food source costs energy; and being out in the open looking for suitable hoarding sites exposes the birds to aerial predators. A good memory for the location of existing caches will avoid hoarding flights to sites that are already occupied and, thus, lower the cost ( $p_c$ ). A recent neurobiological finding lends support to the "distribution" hypothesis for memory. That study (Smulders et al. 1995) found that the volume of the hippocampus of black-capped chickadees (*Parus atricapillus*) is largest in the fall (but not in winter), exactly when memory would be most needed if it were used to distribute caches efficiently.

If it is possible for hoarding to be adaptive without any specialized retrieval mechanisms, it becomes easier to build a plausible scenario for the origin of food hoarding in the Paridae. It is commonly thought that the ancestral social organization of the Paridae is closer to the organization of present-day great tits (*Parus major*) and blue tits (*Parus caeruleus*). In the nonbreeding season, these species live in "basic flocks" with overlapping, nonexclusive home ranges and in groups that can range up to 50 individuals (Ekman 1989; Matthysen 1990). If this was the social organization of the ancestral parids, then one of the assumptions of our model is not met: they do live in winter flocks, but they do not defend winter territories. However this does not seem to be a critical assumption. The effect of not defending a flock territory against neighboring birds comes down to an effective increase in flock size. If a home range is nonexclusive, the number of animals using the same area (and its food supply) increases. It only increases to a finite number, however, still much smaller than the total population size. One of the predictions from the model was that flock size was not important when it came to a hoarding individual invading a population of nonhoarders. So hoarding will be able to establish itself in a population of nonhoarders, even if the social system is less rigid than we first assumed. The hoarding behavior probably evolved out of remote handling of food items (reviewed by Källander and Smith 1990). Leaving items or parts of items at the remote handling site would be enough to start the process proposed by the model if enough of them survive until winter (large  $d$ ) and if they are likely to be found again (large  $r$ ). All bird species in which food hoarding evolved show this pattern of food handling away from the source (Vander Wall 1990).

My model discusses the circumstances under which food hoarding is most likely to evolve. First, the model predicts that as the ratio of hoarded food to naturally available food supply goes up, hoarding is more likely to evolve. This is also advantageous to the hoarding strategy

in an established population of hoarders because it makes it harder for cheaters to persist in the population. The first way in which this ratio can be high is if naturally available food is scarce in winter. Most well-studied Paridae are birds of the temperate zone. The species that live in the regions with the harshest winters (i.e., lowest food availability in winter) hoard the most food and seem to rely most on the hoarded food for their survival (Haftorn 1954, 1956a, 1956b, 1974; Pravosudov 1985; Hampton and Sherry 1992; Brodin 1993). Even within the same species, it has been shown that more northern populations hoard food more intensely than populations in more moderate climates (Brodin et al. 1994). The second way to increase the ratio is to have more hoarded food available. This could be accomplished by hoarding more food to begin with (*h*), by hoarding only those types of food that are durable (*d*), and by hoarding them so they could be found later on (*r*). Since it seems most plausible that in the very beginning not too many items were stored, winters must have been harsh enough to make even a small number of hoards count. In real life, there is also a lower limit of food availability, below which an individual cannot survive winter. If even a little bit of hoarded food brings the availability across that threshold, the selection for food hoarding would be very strong.

Second, the model predicts that once hoarding is established in a population (i.e., hoarding is the resident strategy), the establishment of cheaters will be prevented by keeping the flock size as small as possible. This can be done by defending the home range against other individuals. Ideally, the hoarder would be alone or only with its mate. Some nuthatches (Sittidae), a related family of food-hoarding birds, show such a winter social organization (Matthysen 1993). Why then do many parid species have larger winter flock sizes? Ekman (1989) suggests that many parid species live in a "closed" ecological system. This means that the optimal habitat is saturated with conspecifics and that the only option left over for juvenile birds is to join with others in winter flocks. These juveniles would then pay a price by being subordinate and having less access to resources than the dominant birds in the flock. Removal experiments have provided supportive evidence for the "closed system" hypothesis (Ekman et al. 1981). This constraint would counteract the pressure for smaller flocks brought about by food hoarding. In addition, larger flock sizes could also lead to increased predator vigilance and more efficient foraging through mechanisms like local enhancement (Ekman 1989; Matthysen 1990). Several studies have shown an increase in flock size through both intra- and interspecific flocking as a reaction to harsher weather

(reviewed in Matthysen 1990). The model proposed in this article also predicts that in a population of all hoarders the fitness of any one individual will increase with increasing flock size, provided that the ratio of hoarded to naturally available food is high and that the probability of survival from fall to winter is low (calculations not shown). This makes intuitive sense: if many individuals make caches in the fall, but few survive to winter, more food will be available for the remaining individuals. This becomes especially relevant if the supply of nonhoarded food is low. In contrast, when natural food availability is high relative to hoarded food, having more birds in the flock means having to divide this crop among more individuals. This would decrease the fitness of an individual in that flock. Taking all these factors into account, the final predicted flock size may well be larger than expected from the invasion model alone.

Third, the model predicts that an increasing separation of the foraging and hoarding niches between the flock members is advantageous for hoarding individuals. Niche separation is often found in food-hoarding parid species. Brodin (1994b) found that willow tit (*Parus montanus*) flock members separate their foraging niches along the height of a tree. This separation was even more marked for their hoarding niches. Lens et al. (1994) similarly found that crested tit (*Parus cristatus*) juveniles in the fall hoard their seeds on the outside branches of the trees, even though at the time they are foraging near the trunk. Later on in winter the adults actively prevent the juveniles from foraging near the trunk, thus forcing them to forage where they had previously stored their caches. Andersson and Krebs (1978) also proposed niche separation as a possible mechanism to confer retrieval advantage on the hoarding animal. Although my model clearly states that it is not necessary in order for hoarding to be adaptive, it confirms their prediction that niche separation is beneficial to the evolution of food-hoarding behavior. In the simplified conditions of the model, niche separation does not convey any extra benefits to a nonhoarding population. This is because the food supply is assumed to be equally distributed over the entire flock niche. In real life, certain niches could contain more food than others, and this would make niche separation advantageous to the dominant individuals in a flock. Also, in the model it is assumed that survival is equal for all subniches. In reality, dominant individuals keep subdominants from foraging in the safer niches near the trunks and force them to forage in more exposed sites (Ekman and Askenmo 1984; Hogstad 1988). It is, therefore, not unlikely that there could already have been some form of niche separation even before food hoarding evolved. This would be a case in which the specialized retrieval mechanism al-

ready existed beforehand (for a different reason) and facilitated the evolution of hoarding itself. It could then later have come under the selective influence of hoarding.

This model, even though designed to apply specifically to the Paridae, could also be applied to other groups. The important aspect of the model is that even if some individuals in a population can profit from the actions of a focal individual more than that individual itself—as long as the focal individual profits more from it than the average other individual in the population—its genotype is likely to spread in the population (Maynard Smith 1982). This is similar to the conclusions reached in producer-scrounger games (Caraco and Giraldeau 1991; Vickery et al. 1991). Also, Wilson (1990) discusses an analogous situation from the perspective of multilevel selection. As described above, the focal individual does not need to belong to a well-defined small group. It is enough for it to only interact with a number of individuals that is significantly smaller than the total population size. If this assumption is met, food hoarding will evolve if natural food availability is low, relative to hoarded food. Having

separated foraging niches also increases the probability of evolution of a food-hoarding strategy. Once established in the population, it is to the benefit of the food hoarders to keep the flock size small.

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## APPENDIX A

### Derivation of Mean Payoff

If out of the  $n$  flock members in fall,  $m$  survive until winter (including the focal individual), the fitness of this focal individual is

$$F_{nm} = \frac{f}{m} \times p_s.$$

The probability of  $(m - 1)$  individuals surviving out of  $(n-1)$  original flock members (the focal individual survives by default), given that one individual's survival probability equals  $p_s$ , is expressed by the following equation:

$$\frac{(n - 1)!}{(m - 1)! (n - m)!} (p_s)^{m-1} (1 - p_s)^{n-m}.$$

Therefore, the mean fitness for the focal individual can be expressed as

$$\begin{aligned} F_{nm} &= fp_s \sum_{m=1}^n \frac{(n - 1)!}{(m - 1)! (n - m)!} (p_s)^{m-1} (1 - p_s)^{n-m} \frac{1}{m} \\ &= fp_s \frac{1}{np_s} \sum_{m=1}^n \frac{n!}{m! (n - m)!} (p_s)^m (1 - p_s)^{n-m} \\ &= fp_s \frac{1}{np_s} \left[ \sum_{m=0}^n \frac{n!}{m! (n - m)!} (p_s)^m (1 - p_s)^{n-m} - \frac{n!}{0! n!} (p_s)^0 (1 - p_s)^n \right] \\ &= fp_s \left\{ \frac{1}{np_s} [1 - (1 - p_s)^n] \right\}. \end{aligned}$$

Using analogous reasoning, the other fitness equations can be derived.

## APPENDIX B

## Boundary Values of the Cost of Hoarding for the Simple Case

The boundary below which hoarders can invade a population of nonhoarding individuals is defined by

$$\begin{aligned} F_{\text{nh}} &= F_{\text{hn}} \\ \Leftrightarrow fp_s \left\{ \frac{1}{np_s} [1 - (1 - p_s)^n] \right\} &= (f + hdr) p_s (1 - p_c) \left\{ \frac{1}{np_s} [1 - (1 - p_s)^n] \right\} \\ \Leftrightarrow p_c &= \frac{hdr}{f + hdr}. \end{aligned}$$

The boundary above which nonhoarders can exist in a population of hoarding individuals is defined by

$$\begin{aligned} F_{\text{hh}} &= F_{\text{nh}} \\ \Leftrightarrow (f + nhdr) p_s (1 - p_c) \left\{ \frac{1}{np_s(1 - p_c)} [1 - (1 - p_s(1 - p_c))^n] \right\} &= [f + (n - 1) hdr] p_s \left\{ \frac{1}{np_s(1 - p_c)} [1 - (1 - p_s(1 - p_c))^n] \right\} \\ \Leftrightarrow p_c &= \frac{hdr}{f + hdn}. \end{aligned}$$

## APPENDIX C

## Invasion Conditions in Function of Niche Overlap

The higher the fitness of a hoarding invader is relative to that of the resident nonhoarders, the better its chances are of getting established in the population. To find out how the ratio between the two fitnesses changes with changing niche separation, I calculate the partial derivative of the ratio to  $q$ :

$$\begin{aligned} \frac{F_{\text{hn}}}{F_{\text{nh}}} &= \frac{n(1 - p_c) p_s \left\{ dhr \left[ 1 - \frac{qn - 1}{q(n - 1)} \right] + \frac{1}{np_s} [1 - (1 - p_s)^n] \left[ f + \frac{dhr(qn - 1)}{q(n - 1)} \right] \right\}}{f[1 - (1 - p_s)^n]} \\ &\Rightarrow \frac{\partial \left( \frac{F_{\text{hn}}}{F_{\text{nh}}} \right)}{\partial q} = \frac{dhr(1 - p_c)[1 - (1 - p_s)^n - np_s]}{fq^2(n - 1)[1 - (1 - p_s)^n]} \\ &\leq 0 \text{ (for the range of values relevant in this model).} \end{aligned}$$

The same can be done for the situation of a nonhoarding strategy invading a population of hoarders:

$$\begin{aligned} \frac{F_{\text{nh}}}{F_{\text{hh}}} &= \frac{\{1 - [1 - (1 - p_c) p_s]^n\} \left[ f + \frac{dhr(qn - 1)}{q} \right]}{n(1 - p_c)^2 p_s \left\{ dhr \left[ 1 - \frac{qn - 1}{q(n - 1)} \right] + \frac{1}{n(1 - p_c) p_s} \{1 - [1 - (1 - p_c) p_s]^n\} \left[ f + \frac{dhrn(qn - 1)}{q(n - 1)} \right] \right\}} \\ &\Rightarrow \frac{\partial \left( \frac{F_{\text{nh}}}{F_{\text{hh}}} \right)}{\partial q} = \frac{dhr(n - 1) \{1 - [1 - (1 - p_c) p_s]^n\} (dhrnp_s(n - 1)(1 - p_c) - f\{1 - np_s(1 - p_c) - [1 - (1 - p_c) p_s]^n\})}{(1 - p_c) [fq(n - 1) \{1 - [1 - (1 - p_c) p_s]^n\} + dhrn((qn - 1) \{1 - [1 - (1 - p_c) p_s]^n\} + (1 - q) p_s(1 - p_c))]} \\ &\geq 0 \text{ (for the range of values relevant in this model).} \end{aligned}$$

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