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The Effect of Dominance on Food Hoarding: A Game Theoretical Model

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ABSTRACT: Many food hoarding animals live in small groups structured by rank. The presence of conspecifics in the hoarding area increases the risk of losing stored supplies. The possibility of stealing from others depends on a forager's rank in the group. Highly ranked individuals can steal from subordinates and also protect their own caches. Since storing incurs both costs and benefits, the optimal hoarding investment will differ between individuals of different rank. In a game theoretical model, we investigate how dominant and subordinate individuals should optimize their hoarding effort. Our model imagines animals that are large-scale hoarders in autumn and dependent on stored supplies for winter survival. Many examples can be found in the bird families *Paridae* and *Corvidae*, but the model can be used for any hoarding species that forage in groups. Predictions from the model are as follows: First, subordinates should store more than dominants, but in a predictable environment, this difference will decrease as the environment gets harsher. Under harsh conditions, dominants should store almost as much as subordinates and, later, spend almost as much time retrieving their own caches as subordinates. Second, if on the other hand, bad winter conditions were not expected when storing, dominants should spend more time pilfering caches from subordinates. Third, in populations that are highly dependent on stored supplies, dominants should store relatively more than in populations that are less dependent on stored supplies. Fourth, harsher environments will favor hoarding. And finally, if dominant individuals store, it implies that hoarders have a selfish recovery advantage over conspecific pilferers.

Keywords: food hoarding, dominance rank, game theoretical model, optimization model, foraging theory, behavioral ecology.

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Long-term food hoarding plays an important role for winter survival in many species. Many mammals and birds store large amounts of food in autumn when it is abundant for later consumption during the winter. The percentage of stored food in the winter diet of some birds has been estimated to be 70%–100% in Clark's nutcracker *Nucifraga columbiana* (calculated from Giuntoli and Mewaldt 1978), 25%–85% in the willow tit *Parus montanus* (Nakamura and Wako 1988; Brodin 1994), and >50% in the crested tit *Parus cristatus* (Haftorn 1954). Some hoarding bird species spend the winter in territorial groups that contain unrelated individuals. Examples are the pinyon jay *Gymnorhinus cyanocephalus* (Marzluff and Balda 1992), the Siberian (Ekman et al. 1996) and gray (Waite and Reeve 1993) jays (*Perisoreus infaustus* and *Perisoreus canadensis*, respectively), and most hoarding species of the genus *Paridae*, which consists of tits, titmice, and chickadees (Ekman 1989). Hoarders that forage in groups of conspecifics risk losing stored supplies to competitors in the same gene pool. If the cache pilferer is neither a partner nor a close relative, the cache loss will not be compensated for by any inclusive fitness gain.

Stable winter flocks of this type have a linear dominance hierarchy. Typically, dominants can steal food from subordinates but not vice versa (e.g., Lahti and Rytkönen 1996). Also, dominants can monopolize safe areas and rich food patches in the territory. In some species, it has been shown that dominants exclude subordinates from the most preferred parts of the foraging trees (Ekman and Askenmo 1984; Hogstad 1987; Lens et al. 1994). In such cases, the winter foraging areas will more or less be separated by rank, and the subordinates will rarely visit the dominants' parts of the trees. Henceforth, we will call such rank-specific foraging areas "niches," although they are rank specific rather than species specific.

The positive effect of food stored in autumn and consumed in winter is an increase in winter survival. However, there are also costs of food storing that ultimately may reduce survival, like increased exposure to predators and energy expenditure during storing transports. Loss of stored supplies may also be costly, for example, if supplies are physically defended or if losses are compensated for by ad-

ditional hoarding. If dominants can pilfer from subordinate individuals' supplies without being attacked, they can reduce costs by investing less in their own storing. Since the decision of how much to invest in food storing depends on the balance between the benefits and costs, the optimal storing effort should differ for birds of different rank.

Here, we present a game theoretical model designed to predict rank-dependent hoarding investment in a simplistic two-rank system. Our imagined model animal is a hoarding parid, like the willow tit or the black-capped chickadee *Parus atricapillus*, but the model applies to any hoarding species that lives in stable nonkin groups.

The Model

The model considers the effect of autumn hoarding on fitness. Since there is no reproduction in winter, it is reasonable to model fitness as survival. To reduce the length of this article, we here assume that survival increases linearly with the amount of stored food and present the effect of nonlinearity elsewhere (A. Brodin, K. Lundborg, and C. Clark, unpublished manuscript). Hoarding is not only beneficial but also has costs that reduce survival in proportion to the amount of food stored.

There are two individual ranks, a dominant and a subordinate, each with its own foraging niche within the territory. Such niches could be a subdivision of a group territory into smaller individual areas. Here, we consider the niches to consist of the above mentioned vertical or horizontal separation of foraging trees, such as those that can be seen in several species of hoarding parids (Ekman and Askenmo 1984; Ekman 1990; Hogstad 1992; Lens et al. 1994). In these, the dominants exclude the subordinates from the upper or inner parts of the trees. A system with two ranks is a reasonable simplification of the system in winter flocks of most parids and many corvids (e.g., Ekman 1990; Hogstad 1992; Ekman et al. 1996). Winter flocks are frequently small in hoarding species, and this may enhance the evolution and stability of food hoarding strategies (Smulders 1998).

The dominant can chose to forage in the subordinate's niche but not vice versa. At the beginning of the winter, the amount of stored food will be at its maximum. This means that the optimal option for the dominant is to start in the subordinate's niche and then to switch to its own. Otherwise, the subordinate would reduce the food supply before the dominant could benefit from it. For the subordinate, this is the worst case scenario since loss of food will be at a maximum. After pilfering from the subordinate, the dominant can benefit from the still intact food in its own exclusive niche. The subordinate can only benefit from its own caches and has to accept the dominant's pilfering. We start by assuming that hoarders have no ad-

vantage in relocating their own caches but, later, also investigate the effect of a recovery advantage.

In the autumn, both ranks decide how much food to store. The dominant also must assess how much time it is going to spend foraging in its own and in the subordinate's niche later during retrieval. The total food available for consumption in winter in niche i will consist of stored food, h_i, and food that is present without storing, h_0. We will henceforward call h_0 "background food." The total food available in niche i will then be $h_0 + h_i$ if we, for simplicity, assume that both niches contain equal amounts of background food. Besides cache pilfering by conspecifics of superior rank, there can also be other forms of cache losses, like interspecific pilfering. Scatter-hoarding birds with large winter territories normally experience very low rates of cache loss (Brodin 1993*a*). For simplicity, therefore, we disregard such losses here. The consumption curve of the food supply can be described by e^{-rt}, where r is the depletion rate and t is time spent foraging. If a forager has exclusive access to its own niche, i, the food eaten, g_i, will be

$$g_i = (h_0 + h_i)(1 - e^{-rt}). \tag{1}$$

We can now use equation (1) to make expressions for both ranks. If the dominant starts in the subordinate's niche, the amount of food eaten by the dominant in winter, g_D, will be

$$\begin{aligned} g_D = \frac{1}{2}(h_0 + h_S)\left[1 - e^{-r_2(T-t)}\right] \\ + (h_0 + h_D)(1 - e^{-r_1 t}), \end{aligned} \tag{2}$$

where h_D is the dominant's stores and h_S the subordinate's, T is the total winter time, t is the time the dominant feeds in its own niche, r_2 is the rate of food depletion with two competing foragers present, and r_1 is the rate of food depletion for a single forager, with $r_1 \leqslant r_2 \leqslant 2r_1$. The first term in equation (2) is multiplied by 1/2 since there are two foragers sharing the food. It shows what the dominant gets from foraging in the subordinate's niche. The second term is what it gets from its own niche.

The subordinate gets the same amount of food as the dominant when they both forage in the subordinate's niche. After that, the subordinate may feed on what is left when the dominant has switched to its own niche. With the same notation as above, the food for the subordinate in winter becomes

$$g_{\mathrm{S}} = \frac{1}{2}(h_0 + h_{\mathrm{S}})\left[1 - e^{-r_2(T-t)}\right]$$
$$+ (h_0 + h_{\mathrm{S}})e^{-r_2(T-t)}(1 - e^{-r_1 t}). \tag{3}$$

To get the effect of the act of food hoarding on survival, we must also include the costs, which will be e^{-kh} (app. A). Here, k is a coefficient for the cost of hoarding, and h is the amount of hoarded food. Assuming a linear relationship between the food (g_i) and fitness, the effect of food storing on fitness will be

$$F_{\mathrm{D}}(h_{\mathrm{D}}, t, h_{\mathrm{S}}) = e^{-kh_{\mathrm{D}}}g_{\mathrm{D}}, \tag{4}$$

$$F_{\mathrm{S}}(t, h_{\mathrm{S}}) = e^{-kh_{\mathrm{S}}}g_{\mathrm{S}}, \tag{5}$$

where F_{D} and F_{S} are the fitnesses of the dominant and the subordinate, respectively. To find the optimal hoarding investments, we must maximize these quantities. The dominant optimizes h_{D} and t, whereas the subordinate only optimizes h_{S}. We denote the optima by h_{D}^*, t^*, and h_{S}^*, respectively.

For most cases, h_{D}^* cannot be found analytically (see "Results"). We then use stepwise numerical iteration, although other methods like graphical solutions or partial derivatives may also be possible. The iteration is explained in detail in appendix A and leads to a Nash equilibrium (Nash 1951), that is, a pair of strategies (h_{D}^*, t^*) and (h_{S}^*) that are mutual best replies:

$$F_{\mathrm{D}}(h_{\mathrm{D}}^*, t^*, h_{\mathrm{S}}^*) \geq F_{\mathrm{D}}(h_{\mathrm{D}}, t, h_{\mathrm{S}}^*) \quad \text{for all } h_{\mathrm{D}} \text{ and all } t,$$

$$F_{\mathrm{S}}(t^*, h_{\mathrm{S}}^*) \geq F_{\mathrm{S}}(t^*, h_{\mathrm{S}}) \quad \text{for all } h_{\mathrm{S}}. \tag{6}$$

If there is a recovery advantage for the hoarder, equations (2) and (3) become

$$g_{\mathrm{D}} = \left[\frac{1}{2}h_0 + (1 - p_{\mathrm{h}})h_{\mathrm{S}}\right]\left[1 - e^{-r_2(T-t)}\right]$$
$$+ (h_0 + h_{\mathrm{D}})(1 - e^{-r_1 t}), \tag{7}$$

$$g_{\mathrm{S}} = \left(\frac{1}{2}h_0 + p_{\mathrm{h}}h_{\mathrm{S}}\right)\left[1 - e^{-r_2(T-t)}\right]$$
$$+ (h_0 + h_{\mathrm{S}})e^{-r_2(T-t)}(1 - e^{-r_1 t}) \tag{8}$$

for the dominant and subordinate, respectively. The notation is the same as in equations (2) and (3), except for p_{h}, which is the proportion of caches recovered by a hoarder. The expression $1 - p_{\mathrm{h}}$ is then the proportion taken by the pilfering dominant. Equations (4) and (5)

are still valid expressions for F_{D} and F_{S} if g_{D} and g_{S} are calculated as in equations (7) and (8).

For numerical solutions, the exact values of the parameters are not as important as it is that they are reasonable in relation to each other. The depletion rates, r_1 and r_2, must scale to the chosen time interval, and the coefficient for the cost of hoarding, k, must be reasonable in relation to the number of items hoarded, h_{D} and h_{S}. Also, the relative importance of hoarded food is set by the value of h_0 in relation h_{D} and h_{S}. We scale the parameters according to estimates from the literature. For baseline values of parameters and their justification, see appendix B.

Results

Analytical Solutions of Optimal Hoarding Efforts, h_{S}^* and h_{D}^*

Equilibrium occurs when both ranks store optimally and the dominant's allocation of time between the niches is also optimal. Differentiating F_{S} in equation (5) with respect to h_{S} gives a somewhat surprising result (see app. A). The optimal subordinate hoard size depends on the cost coefficient and food available without storing but not on the time spent pilfering by the dominant:

$$h_{\mathrm{S}}^* = \frac{1}{k} - h_0, \tag{9}$$

provided that this is positive; otherwise, $h_{\mathrm{S}}^* = 0$. The optimum hoard of the dominant is easy to find in the limiting cases, $t = T$ and $t = 0$ (see app. A). In cases when the dominant spends all time in its own niche ($t = T$), the optimal hoarding effort for the dominant, h_{D}^*, is the same as that for the subordinate (eq. [A6]). If the dominant spends all foraging time in the subordinate's niche ($t = 0$), it should not store any food since investment in its own caches cannot increase fitness (eq. [A7]). Since $0 \leq t^* \leq T$, the lowest and highest possible values of the dominant's optimal storing effort are $0 \leq h_{\mathrm{D}}^* \leq h_{\mathrm{S}}^*$, provided that this is positive; otherwise, $h_{\mathrm{S}}^* = 0$.

For the cases when $0 < t < T$, there is one assumption that still makes it possible to find h_{D}^* analytically (app. A): if two foragers deplete a niche at the same rate as one ($r_2 = r_1$), for example, if there is interference. A similar relation as in equation (A6) still holds, but the dominant should now be more sensitive to the costs of hoarding:

$$h_{\mathrm{D}}^* = \frac{1}{2k} - h_0. \tag{10}$$

As expected, the optimal hoard decreases for both categories with an increasing cost or if more food is available

without storing (fig. 1). Unless the dominant decides to spend all time in its own niche, it should store less than the subordinate for any given k or h_0. The straight lines in the bottom panel show that the subordinate (and under the conditions $t = T$ or $r_2 = r_1$, also the dominant) at a given cost of hoarding should aim for a constant total amount of food. If the cost increases, there is an upper limit when no items should be stored. This limit is lower for the dominant than for the subordinate (fig. 1, *top panel*).

Solutions to More Complex Cases of Optimal Hoarding Efforts, h_S^* and h_D^*

For most conditions, h_D^* cannot be found analytically. Inserting the 43.6 d (from eq. [A8]) in equation (4) and iterating the equilibrium (app. A) would give a negative optimum, that is, $h_D^* = 0$. This shows that the dominant should refrain from storing under baseline conditions. However, we assumed that both ranks had equal access to the subordinate's caches. Realistically, a hoarder will find more of it's own caches than a competitor searching more randomly. Considering empirical evidence, we introduce, therefore, a recovery advantage of 4 : 1 for the hoarding subordinate (app. B). Then we can no longer use equation (6) to calculate h_S^*. Instead, we must now include one more factor in our stepwise iteration since h_S^* also depends on t (app. A). With our baseline values, there is a strict Nash equilibrium (e.g., Bulmer 1994) when the dominant stores 22,943 items and spends 79 d in its own niche and the subordinate stores 31,615 items.

Altering Winter Conditions

A simple way to model harsher winter conditions is to decrease background food, h_0. This can be seen either as an environment containing less background food at retrieval or as one requiring more energy for metabolic expenditure, that is, one that is colder. Here "harsher" can mean two different things. First, an environment can be predictably harsh. We investigate this by iterating new equilibria for different values of background food. Starting with no background food, the dominant should store almost as much as the subordinate. As h_0 increases, the dominant should hoard less and spend less time in its own niche (fig. 2, *dashed line*). At some point, we will reach a value of h_0 (around 18,250 with our baseline values) when it no longer pays for the dominant to store. Increasing background food even more now means, instead, that the dominant should spend more time in its own niche (fig. 2, *dashed line*).

Second, when winter arrives, it can be worse than was expected when food was stored in autumn. We model this by allowing the dominant to reoptimize time allocation, t^*, for different values of background food while keeping
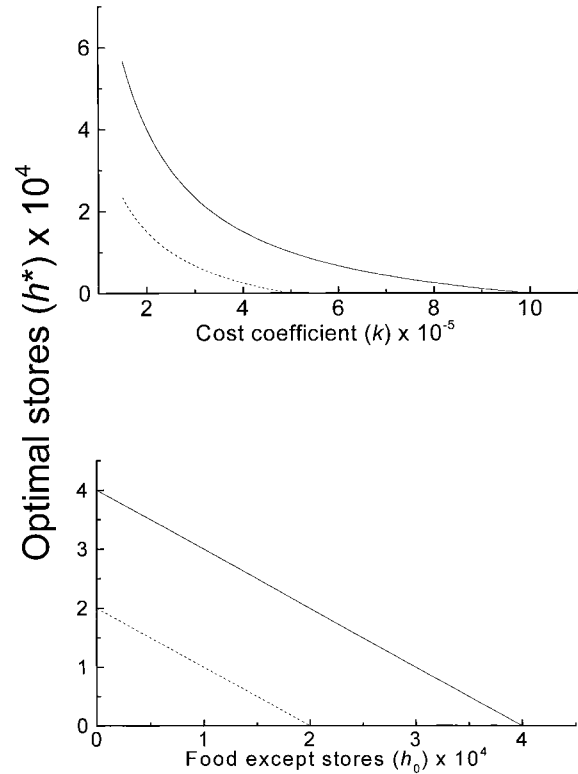

Figure 1: Optimal hoarding effort (h_i^*) as a function of the cost of hoarding (*top panel*) and food availability without stores (*bottom panel*). The solid lines are for the subordinate; and the dashed lines, for the dominant (if $r_2 = r_1$ and $0 < t < T$). If the dominant spends all time in its own niche ($t = 1$), the dominant's optima will be the same as the subordinate's (*solid lines*).

the optimal hoards, h_D^* and h_S^*, constant at the values obtained above for the baseline value of h_0 (10,000). The less background food there is, the less time the dominant should spend in its own habitat (fig. 2, *solid line*).

If we consider the simultaneous optimization of h_D, h_S, and t again, the retrieval advantage means that changes in h_0 will affect not only h_D^* but also h_S^*. The values of some of the parameters (e.g., k and h_0) are difficult to estimate. Since errors in such estimates will be similar for both ranks, the quotient h_D^*/h_S^* is more robust and empirically testable than predictions of numbers of stored items. At $h_0 = 0$, there is no food available in winter except stores. Then the dominant should store almost as much as the subordinate (fig. 3). As h_0 increases, h_D^* decreases faster than h_S^*, and in accordance with figure 2, we find a value of h_0 over which the dominant should refrain from storing.
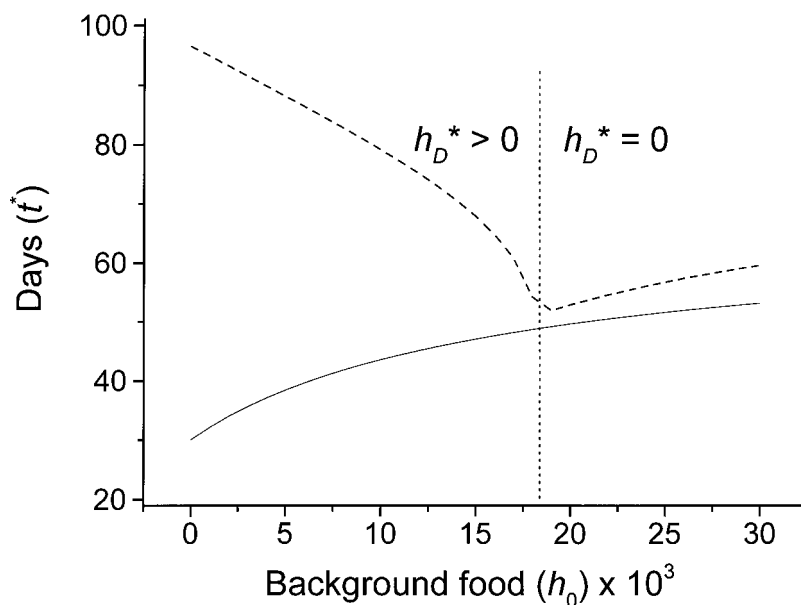
Figure 2: Optimal number of days the dominant should forage in its own niche as a function of the amount of background food, h_0. Decreasing h_0 can be seen as simulating a harsher environment. The predicted response depends on whether a low h_0 was expected (*dashed line*) or not expected (*solid line*). In the former case, less background food will be met by more food hoarding.

The Effect of Other Factors when Reassessing t^* at the Start of Winter

If time is allocated differently in winter than expected during storing, other factors than winter conditions (i.e., background food) should also be considered. It is evident from equation (A8) that the dominant should spend more time in its own niche if the subordinate has stored less than expected (not shown). The effect of prolonging the winter is trivial: if T increases, t increases in a proportional way. If the dominant should experience more interference from the subordinate than previously expected, the emptying rates for two foragers (r_2) will be less than expected. Decreasing r_2 from 0.02 to 0.01 (the same as r_1) means that t^* first decreases to a minimum around $r_2 = 0.0176$ and then increases again (not shown). Values of r_2 below r_1 or above $2 \times r_1$ mean that the dominant should spend even more time in its own niche (not shown).

Discussion

An important message of the model is that dominants should refrain from storing if there is no recovery advantage for hoarders. In a game theoretical model with no dominance asymmetry, Smulders (1998) has shown that a recovery advantage is not necessary for a hoarding strategy to evolve. We do not know of any species in which high-ranked individuals refrain from storing. Our model suggests that there are adaptive mechanisms for cache recovery present, and empirical evidence seems to support this. Such mechanisms could be any of the following: first, a spatial memory for caching locations (e.g., Sherry et al. 1981; Shettleworth and Krebs 1982; Kamil and Balda 1985; Hitchcock and Sherry 1990; Härdling et al. 1995; Healy and Suhonen 1996; Brodin and Kunz 1997; Härdling et al. 1997; Clayton and Dickinson 1998); second, an individually exclusive hoarding area (e.g., Andersson and Krebs 1978); or third, a different individual preference for types of locations (Brodin and Kunz 1997). Such a recovery advantage will have the effect of making caches more individually exclusive. In our model, this will specifically protect the subordinate's caches, but the assumption that separation of caches will promote food hoarding is general and in accordance with earlier models (Andersson and Krebs 1978; Smulders 1998).

Another important message is that the optimal behavior of the dominant under harsh conditions depends on whether such conditions were expected or not. It should store more and forage more in its own niche before a predictably cold winter compared to a more benign environment. Here, our model is in accordance with Smulders (1998), suggesting that more severe (and expected) conditions will promote food hoarding. On the other
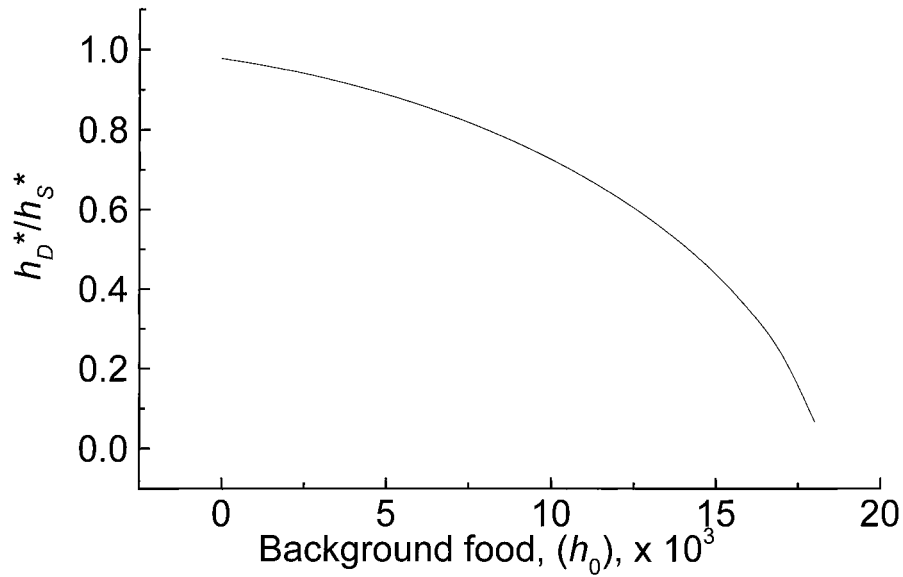
Figure 3: The ratio h_D^*/h_S^* as a function of h_0. It shows how much the dominant should invest in storing relative to the subordinate. In harsh environments (low h_0), dominants should store almost as much as subordinates, whereas they should refrain from storing when winter food is abundant (high h_0).

hand, if the winter unpredictably gets worse than expected, the dominant should spend less time in its own niche. This may seem counterintuitive, but as a result of insufficient hoarding, the dominant's own niche is less valuable than the subordinate's niche. As far as we know, there are no empirical tests of these predictions.

Changing background food, h_0, in relation to the amount of stored food, h, is not only a way to simulate changes in the severity of the climate; it is also a way to compare species that are more or less dependent on stored food in winter. Setting h_0 to 0 will then give predictions for a species that eats only stored food in winter. For species like nutcrackers that are almost entirely dependent on stored food, figure 3 suggests that we would expect birds of different ranks to store almost equal amounts of food in autumn. In parids, on the other hand, where stored food may constitute around 50% of the winter diet, we can expect subordinates to store notably more than dominants.

Under reasonable assumptions, there is only one Nash equilibrium. Both ranks should store, and the subordinate should store more than the dominant since it has to hedge for pilfering. This may seem obvious but has not previously been explicitly stated. There are few empirical studies of hoarding as a function of rank. In willow tits, Lahti and Rytkönen (1996) found that subordinates stored more than dominants during natural foraging. At feeders that were only available for a short time, however, dominants stored more

than subordinates (Lahti et al. 1998). We can also compare this prediction with rank-dependent differences in the regulation of fat reserves. Fat is another way of storing energy for future use but in a shorter time perspective. Ekman and Lilliendahl (1993) found that subordinate willow tits maintained larger fat reserves than dominants. Although fat inside the body cannot be stolen like caches, the underlying mechanism is similar. Dominants have priority when the flock encounters food and, hence, need to invest less in building reserves. In the hoarding case, dominants steal stored food, and in the body fat case, dominants have a more predictable access to food since they can displace subordinates from food sources.

If there is no recovery advantage for hoarders, the optimal hoarding investment for the subordinate, somewhat surprisingly, only depends on the cost of hoarding, k, and the amount of food without stores, h_0. The best behavior for the subordinate is, then, to store, independently of what the dominant does. This prediction results from our simplifying assumption (eqq. [4], [5]) that fitness is proportional to food intake; we will discuss the effects of relaxing this assumption in a future article. Analyzing a symmetrical game with equal players playing "against the field" (but foraging in small groups), Smulders (1998) showed that a hoarding strategy could invade a nonhoarding population even if hoarders do not have a retrieval advantage. The result would be a mixed ESS with hoarders and pilfering nonhoarders.

In reality, such groups will be rank structured, and with the assumptions in our model, pilfering could be an effect of rank rather than a strategy. As mentioned above, however, a hoarding strategy without a retrieval advantage is probably not realistic. The assumptions that made a simple, analytical solution possible for the dominant's optima (and not only for the subordinate's) are even more unrealistic. For example, a dominant will, in reality, probably always visit a subordinate's niche ($t > 0$), at least to sample the foraging possibilities there.

The baseline value of the coefficient for the cost of hoarding, 2.5×10^{-5}, implies a winter mortality of around 40%–50% for hoarding 20,000–30,000 items (app. B). Such high mortality occurs only during severe winters (Jansson et al. 1981), and the costs incurred by hoarding are probably not the only source of mortality. A coefficient of 2.5×10^{-7} would give a mortality of around 5%. According to equation (6), the subordinate could then afford to store over 3 million items. With such a low cost, the limit for hoarding may instead be set by time restrictions. Pravosudov (1985) reported that willow and Siberian tits (*Parus cinctus*) stored 150,000–170,000 spruce seeds in northern Russia. This estimate is considerably higher than others, suggesting that the cost of storing under high food abundance may be very low.

To keep this article at readable length, we have made a number of simplifying assumptions. We think that three of these are worth further investigation: First, realistically, the foragers in autumn will always face uncertainty in h_0. Bet hedging for variation in h_0 will then be better than just using the mean (A. Brodin, K. Lundborg, and C. Clark, unpublished manuscript). Second, the conclusion that the dominant can refrain from storing if there is no retrieval advantage rests on the assumption that there is a subordinate storing. We have not included the possibility that the subordinate could die during the hoarding period. However, according to reasonable assumptions, the loss of the subordinate's stores will be compensated for by the dominant's now exclusive access to all other food in the subordinate's niche (unpublished manuscript). And finally, we have assumed that the effect of food on fitness is linear. This is a reasonable simplification as long as variation is not extreme. With very high and low values of winter food included, a sigmoid effect is more probable.

In conclusion, the model predicts that both low- and high-ranked individuals should store winter supplies if there is separation of caches. The model also suggests that if we observe hoarding by dominant individuals, such a separation (probably consisting of a recovery advantage for hoarders) is present. Further, subordinate birds should store more than dominants, but the difference should be smaller the harsher the environment gets. If conditions at retrieval should be worse than expected when the storing occurred, the dominant should spend more time foraging in the subordinate's niche. Finally, during years of very high food abundance, like extreme mast years, the cost of hoarding might be insignificant.

Acknowledgments

Appendix A

If the cost of hoarding is proportional to the amount of food stored, the fitness loss (L) from hoarding will be

$$L = 1 - e^{-kh} \tag{A1}$$

(modified from Schoener 1971). The probability to survive will then be

$$1 - L = e^{-kh}. \tag{A2}$$

From equation (5) we have

$$F_S = e^{-kh_S}\left\{\frac{1}{2}(h_0 + h_S)\left[1 - e^{-r_2(T-t)}\right]\right.$$

$$\left. + (h_0 + h_S)e^{-r_2(T-t)}\left(1 - e^{-r_1 t}\right)\right\}; \tag{A3}$$

differentiating F_S with respect to h_S then gives

$$\frac{dF_S}{dh_S} = \frac{1}{2}e^{-kh_S}\left[-1 - e^{-r_2(T-t)} + 2e^{-r_2(T-t)}e^{-r_1 t}\right]$$

$$(kh_0 + kh_S - 1); \tag{A4}$$

setting $dF_S/dh_S = 0$ gives optimum hoard size

$$h_S^* = -\frac{kh_0 - 1}{k} = \frac{1}{k} - h_0. \tag{A5}$$

If the dominant decides to spend all foraging time in either niche, we have the two limiting cases, $t = T$ and $t = 0$. If $t = T$, the first term in equation (2) becomes 0, and the optimization is, then, analogous to the one in equations (A3)–(A5):

$$h_{D(t=T)}^* = \frac{1}{k} - h_0. \tag{A6}$$

In the second case, when $t = 0$, there is no h_D for which to solve since the dominant does not spend any time in its own niche:

$$h^*_{D(t=0)} = 0. \tag{A7}$$

In cases when $0 < t < T$, we need an expression for the optimal time spent foraging in the dominant's own niche, t^*. Differentiating a given amount of food, g_D, with respect to t and setting this equal to 0 gives

$$t^* = \frac{\ln\left[2\frac{r_1(h_0+h_D)}{r_2(h_0+h_S)}\right] + r_2 T}{r_1 + r_2}. \tag{A8}$$

With this cumbersome expression for time, there is only one assumption that makes it possible to solve h^*_D analytically for $0 < t < T$. If the interaction between the foragers is strong enough to make $r_2 = r_1$, we have for the dominant:

$$F_D = e^{-kh_D}\left\{\frac{1}{2}(h_0 + h_S)\left[1 - e^{-r(T-t)}\right]\right.$$

$$\left. + (h_0 + h_D)(1 - e^{-rt})\right\}. \tag{A9}$$

Inserting equations (5) and (A8) into equation (A9) gives

$$F_D = e^{-kh_D}\left(\frac{1 - e^{-r\{T-(1/2)[(\alpha+Tr)/r]\}}}{2k}\right.$$

$$\left. + (h_0 + h_D)\left[1 - e^{[-(1/2)\alpha-(1/2)Tr]}\right]\right), \tag{A10}$$

where $\alpha = \ln[2(h_0 + h_D)k]$. Setting $dF_D/dh_D = 0$ then gives two solutions for h^*_D:

$$h^*_D = \frac{1}{2k} - h_0 \text{ and } h^*_D = \frac{2[e^{-(1/2)Tr}]^2}{k}, \tag{A11}$$

of which the first is a maximum. For most cases, however, the dominant's optima must be iterated stepwise. Taking h_S from equation (6), we start with $t = 43.6$ from equation (A8), insert this into equation (4), differentiate this with respect to h_D, and calculate the maximum. We then take the new value of h_D, insert it into equation (2), and differentiate this with respect to t. After the derivation, we calculate the maximum t and insert this again in equation (4)

and so on: $h_D \rightarrow t \rightarrow h_D \rightarrow t \rightarrow h_D$ until we reach an equilibrium.

If there is a recovery advantage for a hoarder, the optimum hoard for the subordinate is obtained from inserting equation (8) into equation (5). Then the subordinate's optimum must also be iterated since $dF_S/dh_S = 0$ gives a useless and complicated expression (not shown). The stepwise iteration is analogous with the one above, except that h_S also must be included: $h_S \rightarrow h_D \rightarrow t \rightarrow h_S \rightarrow h_D \rightarrow t \dots$ until we reach the stable equilibrium (eq. [6]). With our baseline values, this is at $h^*_D \approx 22,943$, $t^* \approx 79.2$, and $h^*_S \approx 31,615$.

Appendix B

We simulate a winter of 100 d, so $T = 100$ and $0 \leqslant t \leqslant 100$. If we assume that 80% of the available food will be consumed during the whole winter, the amount left at the end of winter will be 20%. The slope for an exponential depletion rate can then be found from $e^{-rT} = 0.2$, giving an r of approximately 0.016. Since two individuals should deplete a patch faster than one, we start with $r_1 = 0.01$ and $r_2 = 0.02$.

Nutcrackers have been estimated to make around 10,000 caches in one autumn (Tomback 1982). Parids like the willow tit, the marsh tit *Parus palustris*, the coal tit *Parus ater*, and the crested tit have been estimated to store between 40,000 and 80,000 items (Haftorn 1959; Brodin 1994). We assume that the optimal storing effort will lie between 0 and 50,000 items. Some caches will be left or forgotten, and since we want cached food to be at least 50% of the winter food, we start by setting h_0 to 10,000.

The cost of hoarding is difficult to assess but will have strong effects on the predictions of the model. From equation (9), hoarding 30,000 items would give $k = 2.5 \times 10^{-5}$ for the subordinate. Hoarding 20,000 items would give the same value of k for the dominant (eq. [10]). Winter survival, S_W, can then be calculated from logging both sides of $S_W = e^{-kh}$. For the subordinate, the probability of surviving the winter is then 0.47; for the dominant, 0.61. Such mortality is normal during cold winters in species like willow and crested tits (Jansson et al. 1981).

With the technique of radio-ptilochronology (Brodin 1993b), it has been possible to precisely estimate how large a proportion of their own caches that hoarders recover and how much that other flock members steal. In willow tits and Siberian jays, hoarders found five to seven times as much of their own caches as pilferers did (Brodin and Ekman 1994; Ekman et al. 1996). To be on the conservative side, we set the proportion of caches found by the hoarder, p_h, to 0.8.

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