

# Avian prey-dropping behavior. I. The effects of prey characteristics and prey loss

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Numerous species of birds break hard-shelled prey items by dropping them from a height. This intriguing prey-extraction method provides an excellent opportunity for studying foraging behavior because a single, easily measurable quantity—height of drop—may be influenced by a wide variety of identifiable characteristics of the prey (e.g., breakability, weight) and social environment (e.g., alone or in the presence of kleptoparasites). Using a dynamic, state variable modeling approach, this paper presents the first theoretical framework for avian prey-dropping systems that incorporates the diversity of prey characteristics and social situations. The model yielded a series of qualitative predictions about prey-dropping behavior that can be tested readily in any prey-dropping system. In particular, the results indicated that quantitative and qualitative differences in item breakability and potential kleptoparasitism should have a significant effect on the height and pattern of prey dropping. *Key words:* dynamic state variable model, foraging behavior, kleptoparasitism, prey dropping. [*Behav Ecol* 10:213–219 (1999)]

One of the classic examples of optimal foraging behavior is the breaking of whelks by northwestern crows, *Corvus caurinus* (Zach, 1978, 1979). By dropping a hard-shelled whelk repeatedly onto a hard surface, these crows crack the whelk's shell and expose its edible interior. Northwestern crows dropped whelks from near the height that minimized the total height required to break a whelk, behavior that minimized energy output and supported the predictions of optimal foraging theory (Zach, 1979; but see Plowright et al., 1989).

Avian prey-dropping is an ideal behavior for investigating foraging questions. The foraging task is well defined: the individual must find an appropriate prey item, locate a suitable site for dropping, and choose a height that is sufficient for breaking the prey item (Richardson and Verbeek, 1986, 1987; Wunderle, 1991; Zach and Smith, 1981). Also, researchers can easily measure both the behavior (i.e., the height of drop) and the factors that influence the behavior (e.g., breakability of the prey). Further, prey-dropping behavior is widespread. Twenty-three species of birds, representing three different orders, have been reported to break open a wide range of hard-shelled prey by dropping (reviewed in Cristol and Switzer, 1999).

In the northwestern crow–whelk system, the birds fed alone on defended breeding territories, dropped a very narrow range of prey sizes of a single species of whelk, and always used flat rocks for a breaking substrate (Zach, 1978, 1979). Other prey-dropping systems differ considerably. For instance, many prey-dropping birds forage in groups, thereby facing potential kleptoparasitism (Brockmann and Barnard, 1979), which is not a factor when solitary individuals drop prey. Also, although most of the prey items birds drop share the feature of having a hard, but breakable, outer shell (Cristol and Switzer, 1999), different types of prey may differ in how easily the outer shell breaks. In addition to such quantitative differences in breakability, prey types may differ qualitatively in how they break: some prey items become increasingly more likely to break with subsequent drops (Cristol and Switzer, 1999), while others have the same probability of breaking regardless of how many times they have been dropped (Whiteley et al.,

1990; Zach, 1979). Further, different habitats will provide different substrates of varying hardness, and even within the same foraging area, individuals may have several substrates available for dropping (Barash et al., 1975; Beck, 1980; Zach and Smith, 1981). For example, carrion crows (*Corvus corone*) at one site in Scotland dropped mussels on sand, mussel beds, and a concrete airport runway (Whiteley et al., 1990). Clearly, how easily a prey item breaks will depend on the hardness and texture of the substrate.

Because prey dropping occurs in many bird species and habitats, with a variety of food items, and under different social conditions, it is difficult to predict intuitively how a specific factor should affect prey-dropping behavior. For example, should a bird drop a large and sturdy prey item from a greater height, or would this unduly increase the probability of losing valuable prey through kleptoparasitism? Constructing a mathematical model provides a solution to this problem; with a model, one can manipulate single factors or groups of factors to generate testable predictions. Previous models of avian prey-dropping (Plowright et al., 1989; Zach, 1979) have focused only on a single species and prey item—northwestern crows dropping whelks. To further our understanding of this intriguing behavior, we must develop a theoretical framework general enough to encompass the large range of conditions found both within and among prey-dropping systems. We present a dynamic, state variable model that extends earlier investigations by incorporating differences in the hardness of the substrate and the risk of losing dropped items (e.g., through kleptoparasitism), as well as including a variety of characteristics of the prey. The results of the model provide a series of qualitative predictions that can be tested in any prey-dropping system. In a companion paper we test the predictions of this model using a newly described avian prey-dropping system, that of American crows, *Corvus brachyrhynchos hesperis*, dropping walnuts, *Juglans regia* and *Juglans hindsii* (Cristol and Switzer, 1999).

## THE MODEL

### General modeling approach

We chose to use a dynamic, state variable model (Mangel and Clark, 1988) to investigate food-dropping behavior. A dynamic model allowed us to investigate the probabilistic events (i.e.,

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breaking and/or losing the food item) and sequences of behaviors (i.e., drops) that are inherent in prey-dropping systems.

Using the model, we investigated differences in prey items, habitats, and social environments. Prey items may differ with respect to the energy they contain, their physical dimensions and weight, how easily they break, and whether the number of previous drops affects the probability of breaking. Our model allowed us to vary the energy value and the probability that different food items would break. To examine the effects of different sizes and weights of food items, we assumed that birds carrying larger or heavier items incurred greater flight costs. Items dropped on hard surfaces are more likely to break than those dropped on soft surfaces, so we examined the effect of surface hardness by varying the probability that a food item broke from a given height. We considered loss of food items due to kleptoparasitism or other causes by including a probability that a food item would not be retrieved. This probability of loss is likely to vary depending on the cleanliness of drop areas or the presence of kleptoparasites.

### Model description

We have divided our description of the model into two sections, distinguished by whether the probability of the food item breaking is independent of or dependent on the number of times the item has been dropped previously. Within each of these sections, we consider three situations with regard to the probability of loss: no loss, fixed loss, and height-dependent loss (see below).

#### Probability of breaking independent of previous drops

1. No loss case. In the simplest situation, an individual has a food item that it cannot lose, and the probability of breaking open the food item is independent of the number of times it has been dropped previously. As a necessary simplification for the model, we assumed that the individual has a set number of drops,  $D$ , in which to break the food item open. If the food item is not open after  $D$ , the maximum number of drops, the bird gets no reward from the food. Hence, the expected energy value from the food item at  $D$  is

$$E(D) = 0. \quad (1)$$

In most situations, birds would not have a finite number of drops to break open a food item, so we set  $D$  very high to separate any effects of this assumption from the initial drop behavior in which we were interested (see Results).

For all drops prior to  $D$ , an individual may drop its food item from any height,  $h$ , with  $h$  ranging from 0 to  $h_{\max}$ . A food item dropped from  $h$  will break with probability  $P_b(h)$ , with  $P_b(h)$  obtained from the following equation (Plowright et al., 1989):

$$P_b(h) = 1 - \exp(-kh^{1.5}) \quad (2)$$

where  $k$  is a constant that includes the acceleration due to gravity and the mass of the food item. Equation 2 assumes that there is an increasing chance of the item breaking with increasing momentum and that air resistance has a negligible effect on the velocity of the dropped food item. This equation provides an excellent description for the probability of breaking wheels reported by Zach (1979; see also Plowright et al., 1989). The individual drops at the height that maximizes the expected energy function

$$E(d, D) = \text{maximum expected energy from drop } d \text{ to } D \quad (3)$$

If the food item breaks, the individual gets a net energy amount

$$E_{\text{break}} = E_f - ah - s, \quad (4)$$

where  $E_f$  refers to the total energy from the food item,  $a$  is the energetic cost per unit height of flight, and  $s$  is the energetic cost of finding and examining the food item after a drop (Plowright et al., 1989). If the food item does not break, it receives

$$E_{\text{intact}} = -ah - s. \quad (5)$$

Therefore, for each drop, the food item may break with probability  $P_b(h)$ , with the individual receiving the net energy  $E_{\text{break}}$ . Alternatively, the food item may not break [with probability  $1 - P_b(h)$ ], and the individual receives the net energy of  $E_{\text{intact}}$  plus the maximum energy it can expect from having the food item from drop  $d + 1$  to  $D$ . Thus, the dynamic programming equation is

$$E(d, D) = \max_h \{P_b(h)E_{\text{break}} + [1 - P_b(h)] \times [E_{\text{intact}} + E(d + 1, D)]\} \quad (6)$$

The results consist of a single optimal height,  $h^*$ , that satisfies Equation 6 for each  $d$ .

2. Fixed loss case. The fixed loss case treats the situation where the food item may be lost between drops, but the loss is independent of the height from which the item was dropped. For this model, we use logic and equations similar to the no loss case, with the added probability,  $P_l$ , of losing the food item on each drop. Therefore, Equations 1–5 remain the same; however, the dynamic programming equation (Equation 6) needs to be modified to incorporate  $P_l$ .

When the food item is lost, we assume that the individual pays the cost of the drop, but not the cost of handling the food item between drops (i.e.,  $s$ ). Note that this differs from the intact and break situations, which both include locating and examining the food item. By eliminating  $s$  in prey loss situations, our model more closely describes loss due to kleptoparasitism (where the item is quickly and visibly stolen after the drop) than loss due to a "cluttered area" (which may require more searching). Therefore, the net energy value to an individual that loses its food item is

$$E_{\text{lost}} = -ah \quad (7)$$

We tested the effect of our kleptoparasitism emphasis by incorporating  $s$  into Equation 7 and found no qualitative differences (with values to  $> 10s$ ) or quantitative differences (up to  $2s$  for fixed loss,  $> 10s$  for height-dependent loss). This insensitivity is due to the minimal impact of this handling cost on the results (see Results) and suggests that our emphasis on loss through kleptoparasitism did not affect our results.

For fixed loss, three possibilities exist for an individual dropping a food item: (1) the food item breaks and is not lost; (2) the food item does not break and is not lost; (3) the food item is lost whether it breaks or not. These three possibilities are incorporated in the dynamic programming equation for fixed loss (i.e., each line of the equation below corresponds to one of the possibilities). Thus, the dynamic programming equation for fixed loss becomes

$$E(d, D) = \max_h \{(1 - P_l)P_b(h)E_{\text{break}} + (1 - P_l)[1 - P_b(h)] \times [E_{\text{intact}} + E(d + 1, D)] + P_l E_{\text{lost}}\} \quad (8)$$

3. Height-dependent loss case. The height-dependent loss case is similar to the fixed loss case, but  $P_l$  is now assumed to increase linearly with the height of the drop. Therefore, the probability of losing in the variable loss case is:

$$P_l(h) = \left(\frac{L_{\max}}{h_{\max}}\right)h \quad (9)$$

**Table 1**  
Parameters used in the model and their values for the baseline runs

Parameter	Description	Baseline value
$a$	Cost of flight per unit height	0.00686 <sup>a</sup>
$C_{\max}$	Maximum additional percentage that could be added to the probability of breaking from multiple drops	100 <sup>b</sup>
$D$	Maximum number of drops	60
$E_i$	Energy of prey item	2.04 <sup>a</sup>
$h_{\max}$	Maximum drop height	30 <sup>a</sup>
$k$	Constant in probability of breaking equation (Equation 2)	0.02067 <sup>a</sup>
$L_{\max}$	Maximum probability of losing the prey item for the height-dependent loss case	0.5 <sup>c</sup>
$P_L$	Probability of losing the prey item for the fixed loss case	0.25 <sup>c</sup>
$s$	Cost of searching between drops	0.0426 <sup>a</sup>

<sup>a</sup> Corresponds to value used in Zach (1979) and/or Plowright et al. (1989).

<sup>b</sup> We chose a  $C_{\max}$  for the baseline value that represented a maximum percentage and then investigated the effects of varying this value (see Results).

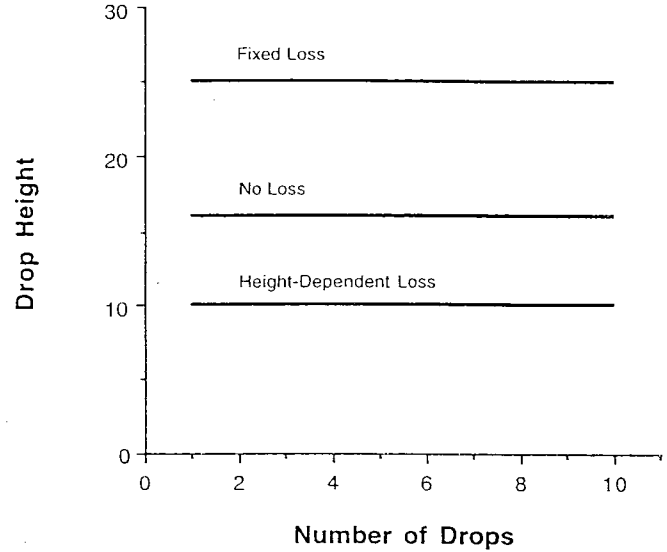
<sup>c</sup> We chose  $L_{\max}$  (0.5) to give a mean  $P_L(h)$  that more or less equals  $P_L$  (0.25) because  $L_{\max}$  will range from 0 at the minimum drop height and 0.5 at the maximum drop height. The qualitative predictions were not affected by this choice of values (i.e., the observed difference increases between the fixed loss and height-dependent loss cases if  $L_{\max}$  is equal for the two cases).

where  $L_{\max}$  is the maximum probability of losing the food item and  $h_{\max}$  is the maximum height from which a food item can be dropped. The dynamic programming equation for the height-dependent loss case matches that of the fixed loss case (Equation 8), with  $P_L$  replaced by  $P_L(h)$ .

#### Probability of breaking dependent on number of previous drops

The previous equations considered food items with probabilities of breaking that were independent of the number of drops. Below, we modify the no loss, fixed loss, and height-dependent loss cases to model food items for which the probability of breaking may be affected by the number of previous drops.

The key change to the equations is modifying the probability of breaking to include the effect of previous drops. Because the probability of breaking increases with the height of the drop, simply considering the number of previous drops may be inappropriate. That is, a previous drop of 20 m will probably have more of an effect on the subsequent probability of breaking than a previous drop of 1 m. Therefore, we assumed that the previous drop heights combined to create a new state variable: the cumulative effect of previous drops,  $C$ . Because previous drops likely will affect types of prey items differently, as a general simplification we assumed that the increase in the probability of breaking that resulted from a previous drop was related linearly to the height of that drop (i.e., a previous drop of 1 m increased  $P_b$  by 0.01). We set a maximum amount,  $C_{\max}$ , that could be added to the breaking probability and assumed that the resulting probability of breaking could not exceed 0.99. Thus,



**Figure 1**

Predicted drop heights for the three loss cases over number of drops, with the probability of breaking unaffected by the number of previous drops. Only drop heights for the first 10 drops are shown.

$$C(d+1) = \begin{cases} = C(d) + h & \text{if } C(d) + h < C_{\max} \\ = C_{\max} & \text{if } C(d) + h \geq C_{\max} \end{cases} \quad (10)$$

and

$$P_b(h, C) = P_b(h) + \frac{C}{100} \quad (11)$$

With this new state variable, the dynamic programming equation for the no loss case becomes:

$$E(C, d, D) = \max_h \{ P_b(h, C) E_{\text{break}} + [1 - P_b(h, C)] [E_{\text{intact}} + E(C + h, d + 1, D)] \} \quad (12)$$

Similarly, the dynamic programming equation for the fixed loss case is

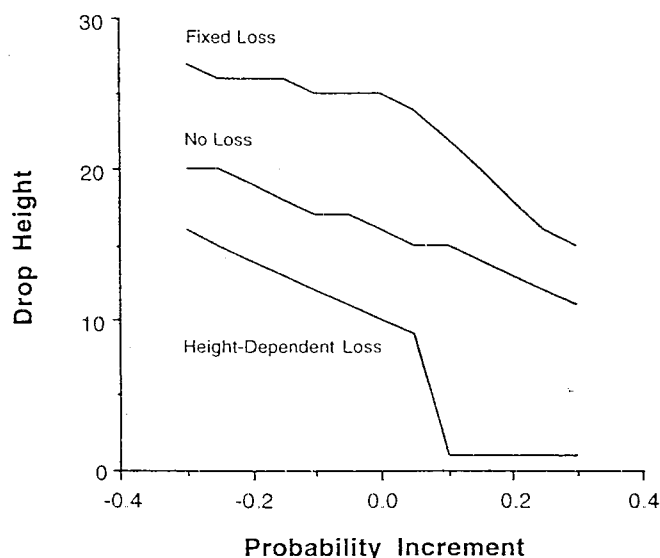
$$E(C, d, D) = \max_h \{ (1 - P_L) P_b(h, C) E_{\text{break}} + (1 - P_L) [1 - P_b(h, C)] \times [E_{\text{intact}} + E(C + h, d + 1, D)] + P_L E_{\text{lost}} \} \quad (13)$$

Again, modifying Equation 13 for the height-dependent loss case requires simply replacing  $P_L$  with  $P_L(h)$ .

## RESULTS

### Probability of breaking independent of previous drops

Using baseline parameters (Table 1), the results predict that drop height will be constant over successive drops but will differ depending on the likelihood of loss and whether the probability of loss is dependent on height (Figure 1). If loss varied with height (height-dependent loss), drop heights were lower than when there was no possibility of loss (no loss); if loss were independent of drop height (fixed loss), drop heights were higher relative to the no loss case. This last, somewhat counterintuitive result of an increased drop height for the fixed loss case can be explained by noting that the



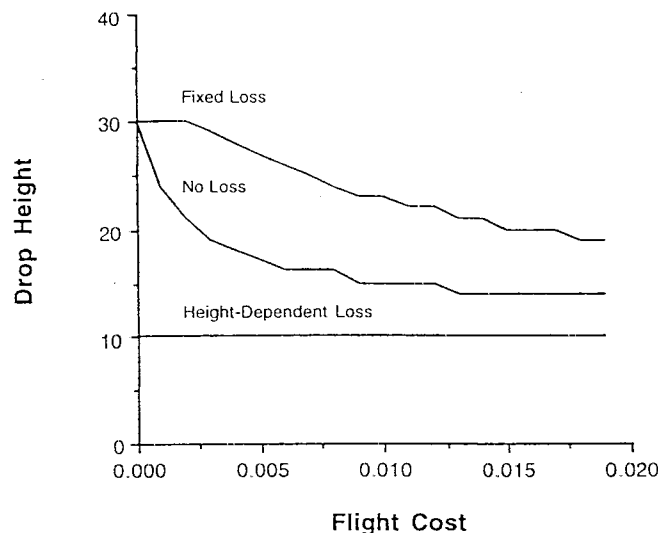
**Figure 2**  
Drop height and increment to the probability of breaking (Equation 2) for the three loss cases. Breaking the food item becomes easier as the probability increment increases.

more times the item is dropped, the greater the chance of loss, and increasing the drop height decreases the number of drops required. The quantitative prediction for the optimal height for the no loss case was 16 m, equivalent to the optimal height determined by Plowright et al. (1989). Additionally, our sensitivity analyses indicated that the qualitative predictions for relative height among the three loss cases were robust to changes in the energy value of the food item ( $E_{\text{intact}}$ ; range: 0–10.1), the handling cost between drops ( $s$ ; range: 0–0.195), the flight cost ( $a$ ; range: 0–0.019), and the probability of breaking the food item at a given height (value from Equation 2 incremented; range:  $\pm 0.3$ ; see below).

Using sensitivity analyses, we first examined the effects on drop height of varying a single characteristic. To investigate how the probability of breaking affected drop height, we either added or subtracted a constant amount from the probability function (Equation 2; e.g., + 0.1 added to the probability of breaking for each height; tested range  $\pm 0.3$ ) and limited the maximum probability of breaking to 0.99. Not surprisingly, drop height decreased as the probability of breaking increased (Figure 2). Thus, the results predict that an individual will use relatively low drop heights when dropping items that are easier to break or when dropping items onto harder surfaces.

We varied the cost of flying per unit height ( $a$ ) to examine the effect of the weight or size of the food item on drop height (Figure 3). For the no loss and fixed loss cases, drop height decreased with increasing flight cost. For the height-dependent loss case, however, the predicted drop height did not change with changes in flight cost. Having the probability of losing the item vary with height apparently overcame the energetic effects of the size of the food item. Therefore, item weight or size may affect drop height, but this depends on the loss case for the study system.

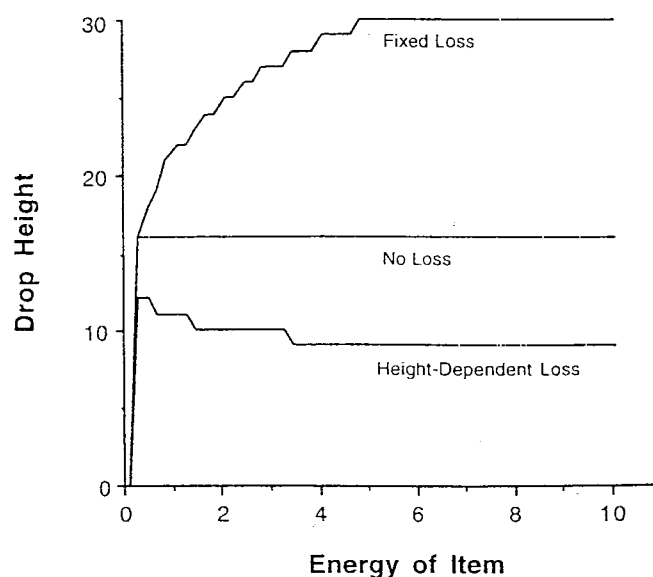
The effect of the energy content of the prey item (prey value) on drop height also differs among loss cases (Figure 4). Each loss case had a certain energy value below which dropping was not profitable. Above this value, drop height remained constant across energy content for the no loss case. For fixed loss, the increase in energy value made the increase



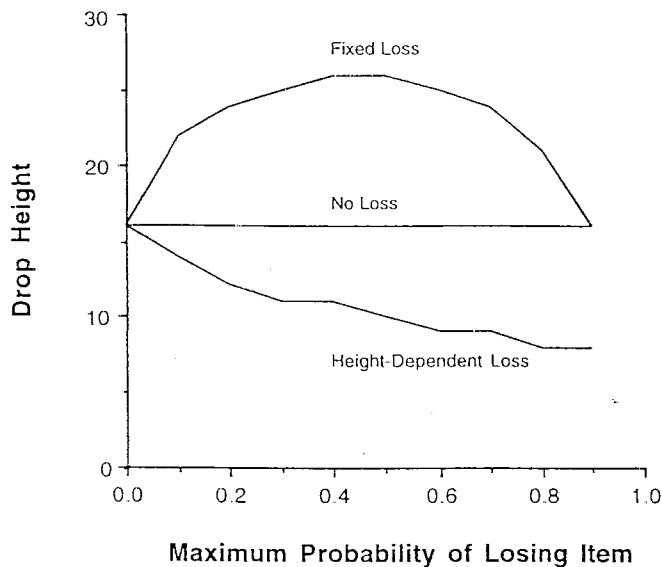
**Figure 3**  
Drop height and flight cost ( $a$ ; Equation 4) for the three loss cases.

in height profitable; this decreased the number of drops necessary and hence the likelihood of losing the prey item. For height-dependent loss, individuals dropped from lower heights to decrease the loss risk. Although dropping lower required more drops to break the prey item, the extra energy value of the prey made this worthwhile; thus drop height decreased with an increase in item energy.

We examined the effect of varying degrees of risk of losing the prey item ( $L_{\text{max}}$ ) on drop height (Figure 5). As the probability of losing the food item increased, the predicted drop height decreased for the height-dependent loss case. Hence, the greater the chance of losing the prey item (e.g., having it stolen), the lower the predicted drop height for this case. For fixed loss, drop heights were relatively greater when a risk of loss was present. Again, this result can be explained by the benefit of minimizing the number of drops required. Interestingly, however, for fixed loss the drop height first increased



**Figure 4**  
Drop height and energy of the food item ( $E_i$ ; Equation 4) for the three loss cases.

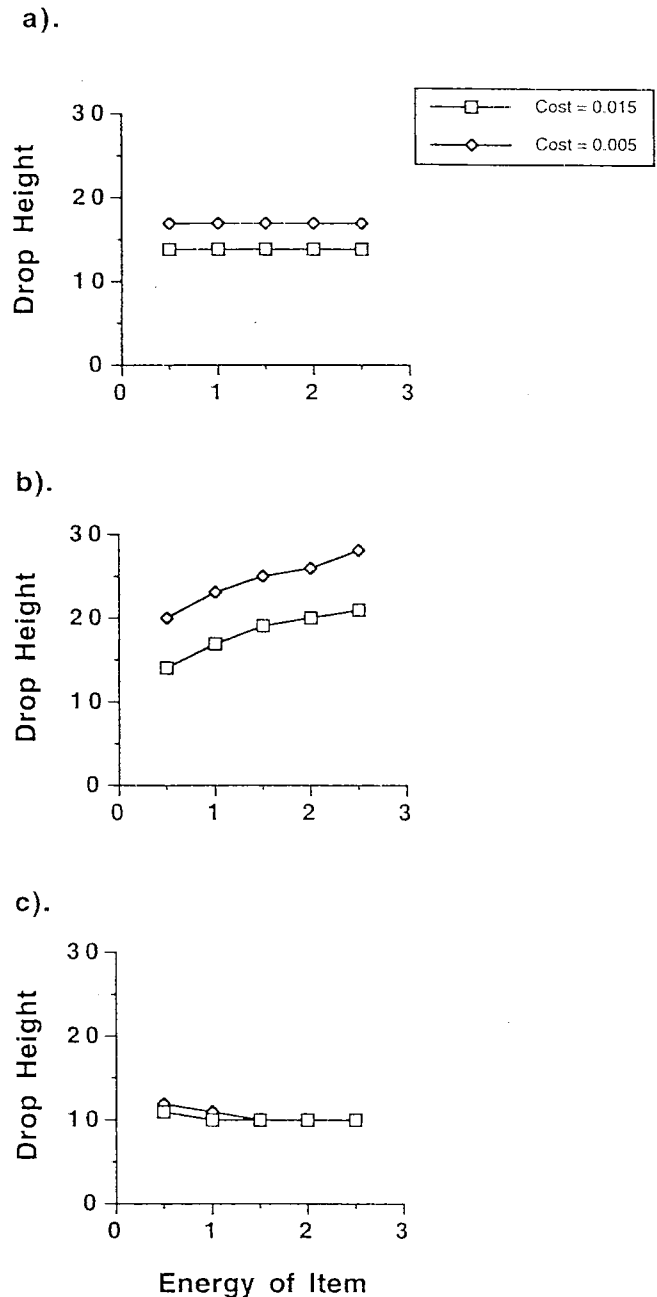


**Figure 5**  
Drop height over the maximum probability of losing the food item ( $L_{max}$ ) for the three loss cases.

with  $L_{max}$  and then decreased. This relationship occurred because the expected energy gain from a prey item decreases as the constant probability of loss increases. That is, if the item is likely to be lost, the expected energy for the item is low. At high probabilities of loss, the expected energy became low enough that the cost of flying ( $a$ ) was relatively big enough to be influential; therefore, drop heights decreased.

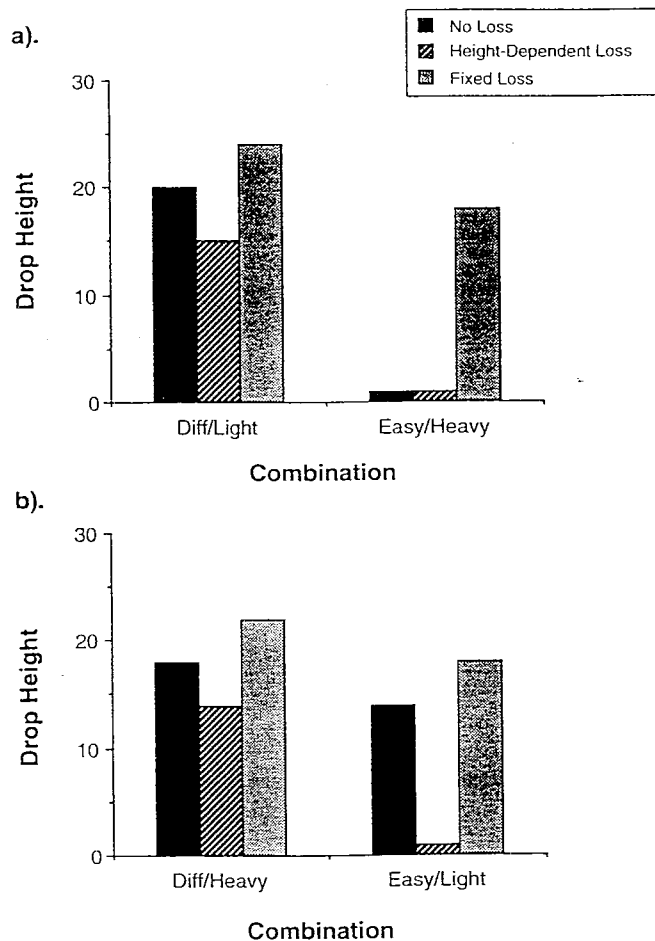
Although these univariate sensitivity analyses predict the impact of changes in single characteristics of avian prey-dropping systems, multivariate approaches can provide more comprehensive predictions in many situations. For example, larger items are likely to increase both flight cost and energy content. Thus, we varied energy content and flight cost simultaneously to see whether the relationship between the two factors would affect relative drop heights for large and small prey items (Figure 6). For this analysis, we assumed that the breakability of small and large prey items was equal (this assumption is relaxed below). For the no loss case, a higher flight cost always resulted in the individual dropping from a lower height, regardless of the energy content of the prey item. With height-dependent loss, the difference in predicted drop height between the two extremes of flight cost was slight over all energy values. Under height-dependent loss, therefore, neither energy content nor flight cost had a significant impact on drop height. Under fixed loss, however, if larger prey items contain significantly more energy, they may be dropped from the same height as smaller prey items of lesser energy content. Thus, under some situations, the increase in energy gained from a large prey item may balance the extra flight cost incurred.

The above analysis assumed that the probability of breaking was not dependent on item size. However, depending on the prey item, this assumption may not be valid. For some mollusk species, the larger individuals break more easily (Siegfried, 1977, Whiteley et al., 1990, Zach, 1979), whereas in others, either smaller individuals break more easily (Maron, 1982) or there is no relationship between item size and breakability (Richardson and Verbeek, 1986). The results described above test the latter situation, where breakability is independent of item size. By using different combinations of flight cost and increment in the probability of breaking (i.e., the amount



**Figure 6**  
Comparison of drop heights when flight cost ( $a$ ) and the energy of the food item were varied simultaneously, but the probability of breaking was independent of item size. Flight costs represent the extremes of a continuum, with 0.005 being extremely light or small items, and 0.015 being extremely heavy or large items. Panels refer to the different loss cases: (a) no loss, (b) fixed loss, and (c) height-dependent loss.

added to Equation 2), we were able to test the two remaining size-breakability relationships in which larger items break more easily or less easily than smaller items. The results yielded qualitative drop height predictions for each situation (Figure 7). As might be expected from previous results, when heavier prey items were easier to break than lighter items (affecting both flight cost and probability of breaking in the same direction), drop heights were lower for heavier prey items. When heavier prey items were more difficult to break,

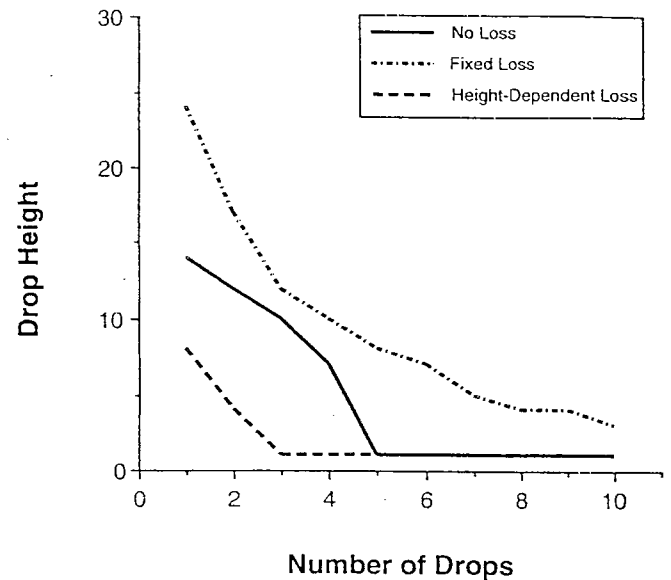


**Figure 7**  
Drop heights for specific combinations of size (weight or physical dimensions) and item breakability. (a) Light items are more difficult to break than heavy items; (b) heavy items are more difficult to break than light items. Parameter values: small item:  $a = 0.005$ ,  $E_i = 1$ ; large item:  $a = 0.015$ ,  $E_i = 2$ .  $P_b(h)$  from Equation 2 was incremented by  $+0.2$  for an easy-to-break item,  $-0.2$  for a difficult-to-break item. Qualitative predictions did not change when energetic values for the two items were varied to the point of being equal.

drop heights were higher for heavier prey items. These predictions were robust to changes in the relative energy of the two food items. The relative qualitative predictions for drop heights (see above) remain unchanged for the no loss, fixed loss, and height-dependent loss cases. The robustness of these predictions was primarily due to the influence of the probability of breaking and the probability of losing the food item, which overwhelmed energetic rewards and flight costs in most circumstances.

#### Probability of breaking dependent on number of previous drops

If the probability of breaking is not affected by the number of drops, the individual was predicted to drop from the same height for all the drops (Figure 1). However, when the probability of breaking increases with the number and height of previous drops, drop height decreased with the number of drops (Figure 8). Varying  $C_{max}$ , the maximum amount that could be added to the breaking probability, did not change the presence of the decline; however, the steepness of the



**Figure 8**  
Drop height over number of drops for the three loss cases when the probability of breaking is dependent on previous drop history. Only drop heights for the first 10 drops are shown.

slope was affected. That is, as  $C_{max}$  decreased, the number of drops until reaching the minimum drop height decreased. As with previous results, the qualitative predictions concerning relative drop height among the no loss, fixed loss, and height-dependent loss cases were not affected by the change in the breaking probability.

## DISCUSSION

To date, most studies of avian prey-dropping have either been anecdotal or descriptive and have lacked a theoretical framework. Our model provides both the framework for studying prey-dropping behavior and a series of qualitative predictions that are readily testable in any prey dropping system. Avian

**Table 2**

Summary of the major qualitative predictions of the model

Characteristic of prey-dropping system	Prediction
Risk of loss increases with drop height	Drop height should decrease with increasing risk of loss
Risk of loss independent of drop height	Drop height should be higher when risk of loss is present
Probability of item breaking is independent of previous drops	Prey should be dropped from a constant height over multiple drops
Probability of item breaking increases with number of previous drops	Drop height should decrease over successive drops
Dropping substrates in foraging area differ in hardness	Prey dropped onto harder surfaces should be dropped from lower heights
Prey types differ in ease of breaking (regardless of size or energy value)	More easily broken prey type should be dropped from lower heights
Prey types differ in size only	Larger prey items should be dropped from lower heights

prey-dropping behavior is extremely widespread and involves a large number of bird and prey species (Cristol and Switzer, 1999). The results of our model indicate that this diversity in predator and prey characteristics should lead to dramatic differences in dropping behavior both within and among systems.

Table 2 summarizes many of the results of the model, listing potential characteristics of different hypothetical study systems and the qualitative predictions that follow from these characteristics. Two of the most robust results were the overriding influences on drop height of both risk of loss and the probability of breaking. The strength of their influence suggests that in many cases these two factors are more responsible for shaping dropping behavior than differences in the energy value of the prey item or the cost of flying. Thus, future studies of dropping behavior should emphasize prey loss and breakability.

Indeed, the results of the model indicate that when armed with two key pieces of information (prey characteristics, loss case), generating and testing the appropriate predictions is a relatively straightforward process. First, one needs information on the characteristics of the prey species that are naturally dropped by the birds. By dropping prey from set heights onto appropriate substrates, one can obtain the probability of breaking as a function of drop height, assess differences in breakability among substrates and prey types (species, size, or weight), and determine whether the probability of breaking changes with subsequent drops. Second, determining the loss case that applies to a particular system requires recording the drop height, kleptoparasitism pressure (if the loss is due to theft), and percentage of prey items lost.

The qualitative nature of the predictions generated by our model facilitates both correlational and experimental tests. Rather than trying to match a specific, predicted drop height with observed behavior (*sensu* Zach 1978, 1979), one can simply compare drop heights under different conditions. The easiest method for testing these qualitative predictions is to observe and compare naturally occurring prey choice and drop behavior. However, specific predictions may also be tested by experimentally presenting the birds with prey items of known characteristics and comparing drop behavior (e.g., Cristol and Switzer, 1999; Maron, 1982).

The predictions of the model concern variation both between distinct avian prey-dropping systems and within the same system. Many of the bird species that drop prey are omnivores (e.g., gulls and crows), and the same individual may be foraging on multiple types of hard-shelled prey in areas with multiple substrates available. Developing appropriate drop behavior under these circumstances is a complicated task. Previous authors have suggested that learning (e.g., operant conditioning and cultural learning) may play a role in dropping behavior (Barash et al., 1975; Beck, 1980; Ingolfson and Estrella, 1978; Maron, 1982; Richardson and Verbeek, 1987; Siegfried, 1977). However, the role of learning in shaping dropping behavior in either simple or more complex situations remains virtually unstudied (but see Beck, 1980). Although our model does not address the ontogeny of dropping behavior, dynamic models can be used to investigate learning behavior. For example, future studies may relax the assumption that the individual knows the value of  $k$  in the probability of breaking equation (Equation 2). Instead, the individual may start with a possible distribution of  $k$  and use their dropping experience to modify their estimate of the parameter for that food item (Hilborn and Mangel, 1997; Luttbeg 1996; Mangel 1990). Our current model does provide the predicted benchmark for fully developed dropping behavior under specified circumstances. Researchers interested in learning can use this benchmark to aid them when investigating the de-

velopment of inexperienced birds into proficient, prey-dropping foragers.

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