Distributing defenses: How resource defendability shapes the optimal response to risk

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Abstract

Many organisms divide limited defenses among heterogeneous assets. Plants allocate defensive chemicals among tissues differing in value, cost of defense, and risk of herbivory. Some ant colonies allocate specialized defenders among multiple nests differing in volume, entrance size, and risk of attack. We develop a general mathematical model to determine the optimal strategy for dividing defenses among assets depending on their value, defendability, and risk of attack. We build upon plant defense theory by focusing on defendability, which we define as the functional relationship between defensive investment and successful defense. We show that if hard-to-defend assets cost more to defend, as assumed in resource defense theory, the optimal strategy allocates more defenses to those assets, regardless of risk. Inspired by cavity-nesting ants, we also consider the possibility that hard-to-defend assets have a lower chance to be successfully defended, even when defensive investment is high. Under this assumption, the optimal response to elevated risk is to reduce defensive allocation to hard-to-defend assets, a conservative strategy previously observed in turtle ants (*Cephalotes*). This new perspective on defendability suggests that, in systems where assets differ in the chance of successful defense, defensive strategies may evolve to be sensitive to risk in surprising ways.

Introduction

For all organisms, defense against predators, parasites or competitors is critical to fitness. Defenses, however, may often be quite costly, in terms of resources allocated, missed opportunities and even potential self-damage (Strauss et al., 2002; Zuk and Stoehr, 2002). This means that the ability to flexibly activate defenses only when they are needed (inducible defenses)—rather than continuously expressing them at a constant level (constitutive defenses)—may be of great benefit (Harvell, 1990). For example, many plants can induce physical and/or chemical defenses in response to herbivore attack (reviewed in Zangerl, 2003), while animals' investment in immune defense may fluctuate, influenced by changing costs and benefits of defense as well as the risk of attack (Viney et al., 2005; Houston et al., 2007; Love et al., 2008). However, the ability to modulate total investment in defense over time is just one way for organisms to respond to environmental variation; another is to change the way defenses are spatially allocated, either across different parts of the organism or across different external resources. For example, some plants reallocate chemical defenses to young leaves, which have greater expected future photosynthetic value than older leaves (van Dam et al., 1996). Individuals may subdivide their time defending multiple mates, multiple food resources, or both (e.g. Camfield, 2006; Buzatto and Machado, 2008; Magellan and Kaiser, 2010). In group-living species such as social insects, birds and primates, different individuals may contribute to defense across multiple food resources (Hölldobler and Lumsden, 1980; Johnson, 1981; Brown, 2013) or multiple nests (Powell and Dornhaus, 2013; Smith et al., 2003; Farabaugh et al., 2010).

Prior theory regarding the defensive behavior of organisms has identified three factors that can influence the optimal deployment of defenses: the costs and benefits of defense and the probability of attack. Optimal plant defense theory was formulated to address the spatial and temporal allocation of defenses within plant tissues or across individuals based on these three factors (McKey, 1979; Zangerl and Rutledge, 1996). Resource defense theory was developed to explain territoriality in animals such as birds and fish: specifically, whether they defend home ranges, food resources, nesting sites and/or mates (Brown, 1964; Grant, 1993). While resource defense theory has focused on the binary choice of whether or not a resource should be defended, plant defense theory has also addressed the optimal allocation of limited defenses across multiple resources. A key concept from resource defense theory is that of economic defendability, which was defined in a binary fashion: a "defendable" territory is one in which the fitness benefits of defending a resource outweigh the costs of doing so (Brown, 1964; Mitani and Rodman, 1979). Plant defense theory has instead considered the optimal spatial allocation of defenses across different tissues, but the focus has been on tissues that vary in their value, affecting the benefit of defense (e.g. McCall and Fordyce, 2010), or in their risk of attack (e.g. Zangerl and Rutledge, 1996)—with no consideration of how tissues may vary in the cost of defense.

Here, we bring a new perspective to the theory of optimal defense by bringing together aspects from plant defense theory and animal-focused resource defense theory in a way that is inspired by collective defense in social insects. Specifically, we broaden the idea of defendability in a way that allows us to examine the consequences of quantitative differences in defensive allocation, by defining it as the functional relationship between defensive investment (cost) and successful defense against an attack (benefit). We consider defendability as a characteristic that may vary among assets, and ask how such variation in defendability influences the optimal spatial allocation of defenses among assets. Often, defendability may vary between assets based on the size of the region that needs to be defended. For territory or resource defense, this is the perimeter of the territory or resource to be defended (Brown, 1964; Grant, 1993; Hölldobler and Lumsden, 1980); it has typically been assumed that the costs of defense scale linearly with the length of the perimeter (Mitani and Rodman, 1979; Lowen and Dunbar, 1994). For chemical defenses in plants, the concentration of the defensive compound within a tissue is generally considered to determine its effectiveness, meaning that the costs of defense scale linearly with tissue volume (van Dam et al., 1996; Iwasa et al., 1996; Brunt et al., 2006). Thus, existing models implicitly assume that assets vary in defendability only according differences in cost; for example, if a hard-to-defend asset costs twice as much to defend as an easy-to-defend asset, this relationship holds regardless of the desired level of defense.

Our approach to defendability, instead, is inspired by the biology of polydomous cavity-nesting ants. In polydomous species, a single colony of ants occupies multiple nests and allocates individuals and resources across these discrete physical locations; such species are widespread geographically and phylogenetically, and are often ecologically dominant or even invasive (Debout et al., 2007). Many of these species nest exclusively in pre-existing natural cavities, such as fallen nuts and beetle-produced cavities in tree stems, often selecting cavities based on specific properties (Herbers, 1989; Powell, 2009; Priest et al., 2021). Some of these species also deploy morphologically and/or behaviorally specialized defenders across nesting cavities to protect these limiting resources from competitors, with the number of defenders depending on cavity properties such as volume, entrance size, and risk of attack (Powell, 2008, 2009; Powell and Dornhaus, 2013; Powell et al., 2017; Fujioka et al., 2019). The multiple nests belonging to a single ant colony may thus be seen as spatially separate assets to be protected, with a limited quotient of specialized defenders that can be divided among those assets according to their value, defendability and risk of attack.

The motivating biological example of allocating specialized defenders across multiple nesting cavities leads us to consider several models of how defendability may vary among assets. In the theory of territory defense, differences in territory defendability are assumed to stem from differences in cost, where cost may scale with territory size in different ways (Hölldobler and Lumsden, 1980; Schoener, 1983). By defining defendability as the functional relationship between defensive investment and successful defense, we are able to encompass not only differences between assets in the cost of defense, but also in the chance that defenses will fail. We begin with the assumption that the chance of successful defense has a sigmoid shape, as is typical in models of anti-predator behavior (e.g. Nonacs and Blumstein, 2010). To illustrate the implications of different assumptions about how assets vary in their relationship between defensive allocation and success, we compare three models of defendability. Two models are based on increasing cost with different scaling relationships, consistent with prior theory developed for territorial defense. In contrast, the third model is tailored to fit the turtle ant *Cephalotes rohweri*, a species of polydomous, cavity-nesting ants in which controlled experiments on defensive allocation and success across nesting cavities have been performed (Powell and Dornhaus, 2013; Powell et al., 2017). The turtle ants (genus *Cephalotes*) typically have a soldier caste that is morphologically specialized for nest defense: large, armor-plated heads are used to physically block small nest entrances from potential intruders (Creighton and Gregg, 1954; de Andrade and Baroni Urbani, 1999; Powell, 2008, 2009, 2016). The number of soldier heads required to block a cavity entrance thus provides a natural index of that cavity's defendability: larger entrances require more soldiers to defend them (Powell, 2008). Based on the natural history of *C. rohweri* as well as previous field experiments, cavities with large entrances are more frequently lost even when well defended (Powell et al., 2017). To capture the non-linear relationship between entrance size and the number of soldiers required, we consider a third model of what makes an asset harder to defend: it is less likely to withstand an attack, even when amply supplied with defenses. We show that a model of defendability in which hard-to-defend assets have a higher chance of defensive failure, unlike one in which successful defense simply costs more, gives rise to an optimal defensive strategy which is conservative in its response to risk—a qualitative response observed in prior experiments with *C. rohweri* (Powell et al., 2017). More generally, our models suggest that defendability plays a key role in optimal defensive allocation among heterogeneous assets, and that systems which differ in the way that defendability varies among assets may have very different defensive responses to risk.

Methods

We describe a mathematical model of the flexible deployment of limited defenses across assets that vary in defendability, risk of attack, and value. The model consists of a set of equations specifying how the allocation of defenses to different assets affects the expected fitness gained from those assets. We define defendability as the chance that an asset can successfully be defended against an attack, based on the quantity of defensive resources allocated there. Assets may vary in their defendability based on physical features such as area (for territory defense), entrance size and number (for nest cavity defense), or tissue volume and toughness (for chemical defenses). We create a defense model as a family of functions mapping defensive allocation to probability of successful defense, indexed by an additional argument (here called perimeter size) that varies across assets, indicating the quantity of defenses required to achieve a certain level of defensive success against a single attack. To explore the consequences of variation in different aspects of defendability, we create three different defense models, based on different assumptions about the relationship between defensive investment and the probability of successful defense across assets that vary in defendability. For each defense model, we describe the optimal defense strategy; that is, given a particular quantity of defensive resources to spread across all assets, which allocation of defenses among assets maximizes the expected fitness gained. To do this, we combine two approaches: we numerically calculate the optimal strategy for several specific examples, and we analyze how the marginal value of additional defenses at an asset is affected by the defense model as well as the characteristics of the asset.

The model framework is designed to be general enough to apply to the allocation of chemical defenses across plant tissues, the allocation of defensive effort across multiple food resources, for example in territorial animals, and the allocation of specialized defenders across nesting resources, for example in polydomous ants. In Supplementary Material S1, we discuss the assumptions of the model and its three variations in more detail, and how well they may apply across different biological scenarios such as the allocation of defensive compounds across leaves based on age (van Dam et al., 1996), defense of multiple food resources by primate groups (Brown, 2013) and social insects (Tanner, 2008; Han and Elgar, 2020), and defense of multiple cavity nests in ants (Powell et al., 2017; Fujioka et al., 2019).

Model definition

The total amount of defense available is formulated as a discrete quantity m, while the number of assets available is denoted n. Each asset i has a value v_i denoting the potential fitness gain from that asset. Defendability (the relationship between defensive allocation and the probability of successful defense against an attack) varies among assets according to the index h_i, which indicates the quantity of defense required to provide a specified level of defensive coverage. For simplicity, we will here refer to h as the perimeter size, referring to the defensive perimeter which is the part of the asset that needs to be defended; this could mean the perimeter of a territory, the area of a nest entrance, or the volume of a leaf. However, other factors such as number of nest entrances or leaf toughness may also influence the amount of defense required at different assets (see Supplementary Material S1 for more detail). Attacks are assumed to occur on each asset independently of one another, at a rate a_i which may vary across assets according to differences in accessibility or attractiveness. These variables and their interpretations are summarized in Table 1.

First of all, we want to model defendability: the probability of successful defense against a single attack, depending on the defensive resources dedicated to a particular asset and its perimeter size. We model the relationship between the defensive allocation, k, and the

Table 1
Asset characteristics: definitions and variables

Concept	General interpretation	In turtle ant nest defense	In the model
Defendability	Functional relationship between defensive investment & success	Probability of defending a nest against a single attack, depending on number of soldiers	$d(k, h)$
Perimeter size	Size of the region of the asset to be defended	Nest entrance size	h
Value	Potential fitness gain from an asset	Nest volume (brood capacity)	v
Risk	Rate of attack	Expected number of attacks per cavity per season	a

Note: See text and Supplementary Material S1 for interpretations in other specific systems, such as plant defense and territory defense

probability of successful defense, $d(k)$, using the logistic function:

$$d(k) = \frac{A}{1 + e^{-S(k-M)}}. \tag{1}$$

This function has a customizable sigmoid shape controlled by three parameters: A is the upper asymptote (the lower asymptote is always zero), S reflects the steepness of the curve, and M is the midpoint, which is the point of greatest steepness. In our application, A is the chance of successful defense when there are plenty of defenses, S controls the marginal value of additional defenses (i.e. how much each defensive unit contributes to defense), and M is the number of defensive units at which that marginal value is maximized. We consider three different defense models, which differ in the way that the parameters A, S, and M relate to perimeter size h.

Defendability: coverage model

For the simplest defense model, we begin with a natural assumption: what determines the probability of successful defense is simply the defensive coverage, that is, the ratio between the number of defensive units allocated and the perimeter size. We use the following defense function to model the chance that k defensive units successfully defend an asset with perimeter size h against a single attack:

$$d_0(k, h) = \frac{1}{1 + e^{-\frac{\alpha}{h}(k-h)}} \tag{2}$$

(see Figure 1a). In this version of the generalized logistic function, the midpoint $M = h$, the steepness $S = \alpha/h$, and the asymptote $A = 1$. Because the function only depends on the ratio $k{:}h$, under this model five defensive units at an asset with perimeter size $h = 5$ are exactly as effective as one defensive unit at an asset with perimeter size $h = 1$. The model has one parameter, α, which affects the steepness and thus the marginal value of additional defenses. For $\alpha = 5$, at an asset with perimeter size $h = 1$, the chance of success with no defense is close to zero, with one defense unit is 50%, and with two units is close to 100%.

Defendability: accelerating-cost model

Next, we consider the possibility that the defensive resources needed are not directly proportional to perimeter size, but increase more than proportionally as the perimeter size increases. To model this, we modify the defense function as follows:

$$d_1(k, h) = \frac{1}{1 + e^{-\frac{\alpha}{h^\beta}(k-h^\beta)}} \tag{3}$$

(see Figure 1b). The model has one additional parameter beyond the coverage model, β, which controls how quickly defensive costs increase as perimeter size increases. We assume that $\beta > 1$; for $\beta = 1$, $d_1(k, h)$ reduces to the coverage model, $d_0(k, h)$. In the accelerating-cost model, the midpoint and the steepness depend on a power of the perimeter size ($M = h^\beta$ and $S = \frac{\alpha}{h^\beta}$), but the asymptote A is still equal to 1 regardless of perimeter size. In contrast to the coverage model, five defensive units at an asset with perimeter size $h = 5$ are not as effective as one defensive unit at an asset with perimeter size $h = 1$. For $\beta = \log 6/\log 5$, six

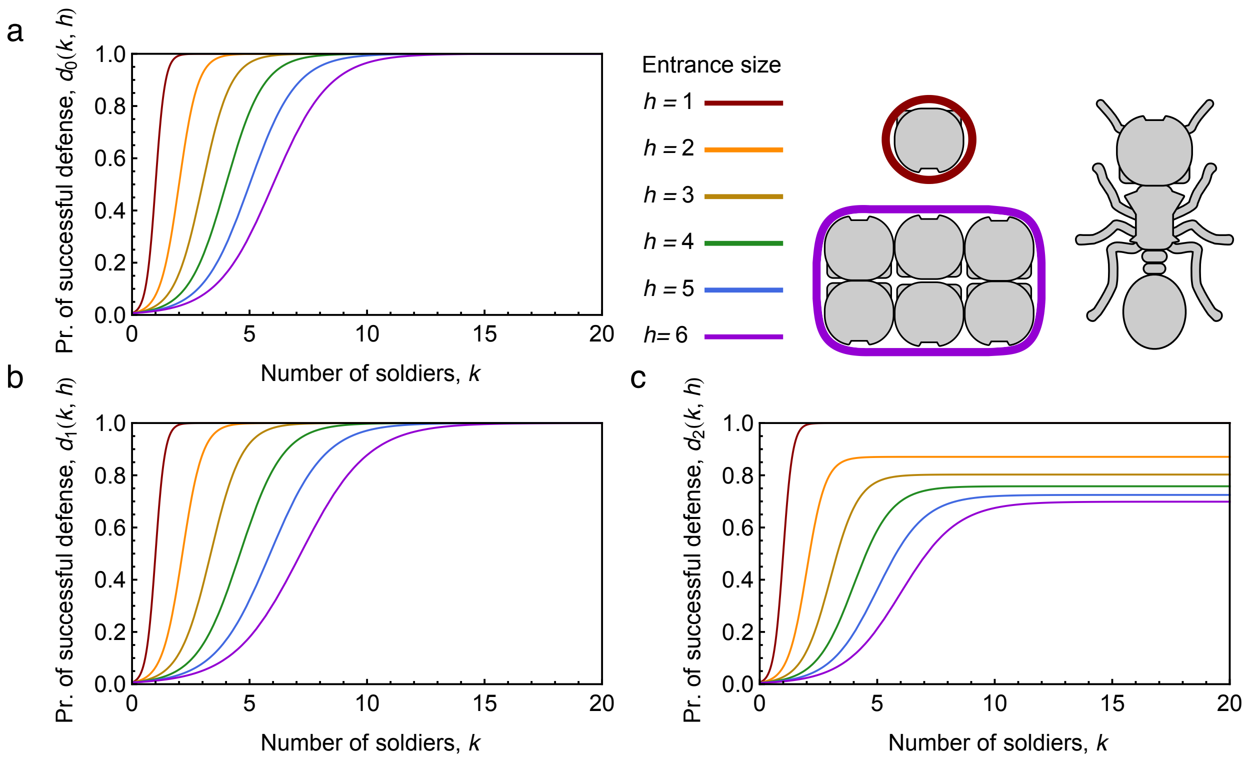

Figure 1
Three defense functions, illustrated for turtle ants. The defense function describes the probability that k defensive soldiers can successfully defend a single nest cavity with entrance size h against a single attack. In three models, each based on the logistic curve, the number of soldiers required to defend a nest cavity increases with entrance size. (a) In the coverage model $d_0(k, h)$ that increase is directly proportional to entrance size. (b) In the accelerating-cost model $d_1(k, h)$, the number of soldiers required increases faster than entrance size (see Equation 3; here, $\beta = 1.11328$). (c) In the diminishing-success model $d_2(k, h)$, even with many soldiers a large-entrance nest cavity can never be defended as well as a small-entrance nest cavity (see Equation 4; here $\gamma = 0.2$). Defensive soldier heads of *C. rohweri* blocking a small entrance ($h = 1$) and a large entrance ($h = 6$) are illustrated.

defensive units at an asset with perimeter size $h = 5$ are just as effective as one defensive unit at an asset with perimeter size $h = 1$ (that is, if $h = 5$ then $h^\beta = 6$).

Defendability: diminished-success model

Finally, we consider the possibility that some assets can never be defended as well as others, regardless of how much defensive effort is allocated to them. To model this, we modify the defense function as follows:

$$d_2(k, h) = \frac{h^{-\gamma}}{1 + e^{-\frac{\alpha}{h}(k-h)}} \tag{4}$$

(see Figure 1c). This model has one additional parameter beyond the coverage model, γ, which controls the asymptote. We assume that $\gamma > 0$ (for $\gamma = 0$, this reduces to the coverage model, $d_0(k, h)$) and that $h \geq 1$. In this third version, as for the first, the midpoint and the steepness depend directly on the size of the region to be defended ($M = h$ and $S = \alpha/h$); however, here the asymptote also decreases with the size of the region to be defended ($A = h^{-\gamma}$). The result is that, just as for $d_1(k, h)$, five defensive units at an asset with perimeter size $h = 5$ are not as effective as one defensive unit at an asset with perimeter size $h = 1$. For $\gamma = 1/5$, six defensive units at an asset with perimeter size $h = 5$ are about as effective as one defensive unit at an asset with perimeter size $h = 1$ (50%), but no level of defense at an asset with perimeter size $h = 5$ can match the effectiveness of two defensive units at an asset with perimeter size $h = 1$.

Risk of attack

Given the relationship between perimeter size, defensive allocation, and chance of successfully defending against a single attack, we would like to model the chance that a particular defensive allocation can successfully protect a single asset over an entire season. This depends on the number of attacks on that asset during the season. We assume that attacks occur according to a Poisson process with fixed rate a_i, so the rate of successful attacks is also a Poisson process with rate $a_i(1-d(k,h))$, that is, the rate of attack multiplied by the probability of failed defense. The chance that no successful attacks occur over the entire season, on an asset with perimeter size h defended by k defensive units is therefore:

$$s(k,h,a) = e^{-a_i(1-d(k,h))} \tag{5}$$

for any of the three defense functions.

Value

Finally, we want to estimate the potential fitness effects of a specific allocation of defenses among a set of assets that may vary in defendability, risk of attack, and value. We represent an allocation of m defenses among n assets as a vector $\vec{k} = (k_1, k_2, ..., k_n)$ where $\sum_{i=1}^{n} k_i = m$ and each k_i is non-negative. We characterize the n assets available with a vector $\vec{h} = (h_1, h_2, ..., h_n)$ of perimeter sizes, a vector $\vec{a} = (a_1, a_2, ...a_n)$ of attack risks, and a vector $\vec{v} = (v_1, v_2, ..., v_n)$ representing the asset values. For each asset i, we multiply the chance of successfully defending that asset over the whole season, $s(k_i, h_i, a_i)$, by the potential it has to add to fitness, v_i. Then we sum over all available assets

$$f(\vec{k}, \vec{h}, \vec{a}, \vec{v}) = \sum_{i=1}^{n} v_i s(k_i, h_i, a_i) \tag{6}$$

to get the expected fitness for the season.

Numerical examples

To illustrate the way that the optimal strategy depends on the asset features and how this is affected by the defense function, we include three series of numerical examples representing the allocation of turtle ant soldiers among four different potential nest cavities. Each series focuses on the effect of one of the three characteristics of interest: value, defendability, or risk of attack. In each of the numerical examples, we consider two pairs of cavities which differ in just one of those characteristics, e.g. two cavities are of high value and the other two are of low value, while all other characteristics are fixed (see Table 2). Using Mathematica (Wolfram Research, Inc., 2020), we generated all possible ways to divide m soldiers among four nest cavities (where it is possible that some cavities have no soldiers) and asked which of those ways gave the highest expected reproductive fitness (Equation 6) using each of the three defense models. We let the total number of soldiers m vary from 1 to 40 and found the optimal allocation among cavities for each value of m. For all examples, we used model parameters $\alpha = 5$, $\beta = 1.11328$ (accelerating-cost model) and $\gamma = 0.2$ (diminishing-success model), as illustrated in Figure 1. The value $\alpha = 5$ was chosen so that for an entrance size matching one soldier's head, the chance of successful defense with no soldiers is close to zero (Hasegawa, 1993; Powell et al., 2017). The values of β and γ were chosen to facilitate comparison between models: the accelerating-cost and diminishing-success models show approximately equivalent defensive success for six soldiers in cavities with entrance size $h = 5$ (as good as five soldiers in the coverage model), but any soldiers beyond six are less effective in the diminishing-success model than the accelerating-cost model.

Model analysis

Finally, in order to interpret the results of our numerical examples and generalize beyond the specific parameter values we chose, we examined the marginal value of each soldier—how much it contributes to expected colony reproductive fitness, depending on where it is deployed. A necessary (but not sufficient) property of an optimal strategy is that fitness cannot be improved by moving just one soldier from one cavity to another: that is, the marginal value of the last soldier in each cavity is greater than the marginal value of an

Table 2
Parameter settings for numerical examples

Numerical example series	Value	Defendability	Risk of attack
Asset value	$v_H = 50$, $v_L = 10$	$h = 1$	$a = 1$
	$v_H = 50$, $v_L = 10$	$h = 5$	$a = 1$
	$v_H = 50$, $v_L = 10$	$h = 1$	$a = 10$
	$v_H = 50$, $v_L = 10$	$h = 5$	$a = 10$
Asset defendability	$v = 50$	$h_S = 1$, $h_L = 5$	$a = 1$
	$v = 50$	$h_S = 1$, $h_L = 5$	$a = 10$
Risk of attack	$v = 50$	$h = 1$	$a_H = 10$, $a_L = 1$
	$v = 50$	$h = 5$	$a_H = 10$, $a_L = 1$

Note: In each numerical example, we considered four cavities of two different types, with variation in only one characteristic. For example, in the first row, two cavities had value $v_H = 50$ and two had $v_L = 10$, while all four had entrance size $h = 1$ and attack rate $a = 1$. We ran each series for all three defense models, using parameters $\alpha = 5$, $\beta = 1.11328$ and $\gamma = 0.2$

additional soldier in any other cavity. Mathematically, this property can be expressed as:

$$\Delta f(\hat{k}_i, h_i, a_i, v_i) \geq \Delta f(\hat{k}_j + 1, h_j, a_i, v_j) \tag{7}$$

for all cavities i and j with $j \neq i$, where $\hat{k}_i$ represents the number of soldiers in the ith cavity under the optimal deployment strategy. The marginal value of the kth soldier in cavity i is defined as:

$$\Delta f(k_i, h_i, a_i, v_i) = v_i \left(s(k_i, h_i, a_i) - s(k_i - 1, h_i, a_i) \right). \tag{8}$$

By examining the way that the marginal value of each soldier is affected by cavity value v, perimeter size h, and risk of attack a, we gain insight into the way that the optimal allocation of soldiers among cavities is affected by these properties, and how this differs between the three models.

Results

First we illustrate the behavior of the model by describing the results of the numerical examples, based on the allocation of turtle ant soldiers among four nest cavities of two different types. Using each of the three defense models, we show the optimal defense strategy in response to differences in value, defendability and risk of attack, both in terms of which cavities are defended, and how defenses are balanced between cavities. Comparing strategies across the three models, we highlight aspects of the strategy that depend on the assumptions of the specific defense model. Second, we analyze the model more generally to explain why value, defendability and risk of attack affect the optimal defensive strategy in different ways, and why only some aspects of that strategy are affected by the details of the defense model.

Numerical examples

In all cases, below a certain threshold number of soldiers, the optimal strategy is to concentrate soldiers in just a few cavities, rather than spreading them out among all cavities. We can thus define two different colony states, which will depend on the number of soldiers and cavities available, as well as the properties of those cavities: (1) the *defense-limited state*, in which a colony, to perform optimally, must choose the best subset of cavities to defend, and (2) the *asset-limited state*, in which a colony's optimal strategy must balance defenses well among all cavities. In particular, we will focus on two questions: (1) in the defense-limited state, which cavities are defended first? and (2) in the asset-limited state, how are the numbers of soldiers in cavities of each type balanced? The answers to these questions are summarized in Table 3, with features common to all defense models indicated in each table cell and footnotes indicating differences between models. Below, we give more detail for each numerical example.

Table 3
Common features of optimal defensive strategies across models.

	Asset choice, defense limited	Defense allocation, asset limited
Value	high value	equal allocation to high/low value
Defendability	easy-to-defend	greater allocation to hard-to-defend[a,b]
Risk of attack	—[c]	equal allocation to low/high risk[d]

NOTE When given assets of two types, differing in just a single characteristic, the optimal strategy defines both which type will be defended when defenses are limited ("Asset choice, defense limited") and the relative allocation of defenses between those types when assets are limited ("Defense allocation, asset limited").

a In the coverage and diminishing-success models, the optimal allocation ratio is governed by the perimeter size ratio h_L:h_S; in the accelerating-cost model it is governed by the perimeter size ratio raised to a power $(h_L{:}h_S)^\beta$

b In the diminishing-success model, increased risk of attack reduces the optimal allocation to hard-to-defend assets; in the other models risk of attack has no effect.

c In the diminishing-success model, the optimal strategy abandons high-risk, hard-to-defend assets when defenses are limited. In the other models, asset choice depends on the total defense available.

d When cavities are hard to defend, the optimal allocation ratio deviates from 1:1. Under the coverage model and the accelerating-cost model, the ratio favors high-risk assets, while under the diminishing-success model, it favors low-risk assets.

Asset value

When a colony is defense-limited, the optimal strategy leaves one or more cavities undefended; the undefended cavities are always those of low value, regardless of the risk of attack or the defense model (Figure 2). When all nest cavities are easy to defend, and at low risk of attack, a colony is defense-limited if it has fewer than $m = 7$ soldiers (Figure 2a,c, left of the grey vertical line). When there are $m = 7$ soldiers, all four cavities are defended; the optimal allocation across the four cavities is (2,2,2,1), meaning that one of the low-value cavities receives just one soldier. When there are $m = 7$ or more soldiers, the colony is asset-limited, and the optimal strategy is to allocate approximately equal numbers of soldiers to both high- and low-value cavities. This yields an allocation ratio—the average number of soldiers per defended low-value cavity, divided by the average number of soldiers per high-value cavity—

near 1:1 (Figure 2a,c, right of the grey vertical line). As the number of available soldiers increases, each cavity takes turns receiving one soldier, with the high-value cavities given priority. Thus, when the number of soldiers available is not divisible by 4, the allocation ratio is a little below 1. When all nest cavities are hard to defend, but still at low risk of attack, many more soldiers ($m = 30$) are required before the colony becomes asset-limited (Figure 2b,d, vertical grey line). For more than 30 soldiers, the optimal allocation ratio is still approximately 1:1 (Figure 2b,d, right of the grey vertical line), and as the number of available soldiers increases, again each cavity takes turns receiving one soldier. The same general patterns hold for all three defense models, for both low and high risk (see Supplementary Material Figures S1 and S2).

Asset defendability

When a colony is defense-limited, the optimal strategy leaves one or more cavities undefended: when assets vary in defendability, the cavities left undefended are always hard to defend (large-entrance), regardless of the risk of attack or the defense model (Figure 3). In each case, soldiers are initially allocated to the easy-to-defend cavities (allocation ratio = 0); then an increasing number of soldiers is allocated to the first hard-to-defend cavity; then the ratio drops as the second hard-to-defend cavity is added, decreasing the average number of soldiers in each hard-to-defend cavity with soldiers. The vertical grey line indicates the point at which all available cavities are defended, and thus the switch to an asset-limited state. In the asset-limited state, the optimal strategy allocates many more soldiers to the cavities that are hard to defend than to those that are easy to defend. For the coverage model, the allocation ratio peaks at 5:1, regardless of risk, and as the number of soldiers increases beyond 24, additional soldiers are added in the same ratio—one new soldier in each easy-to-defend cavity, followed by five new soldiers in each hard-to-defend cavity (Figure 3a,b). For the accelerating cost model, the peak is at 6:1, regardless of risk, and new soldiers are added in

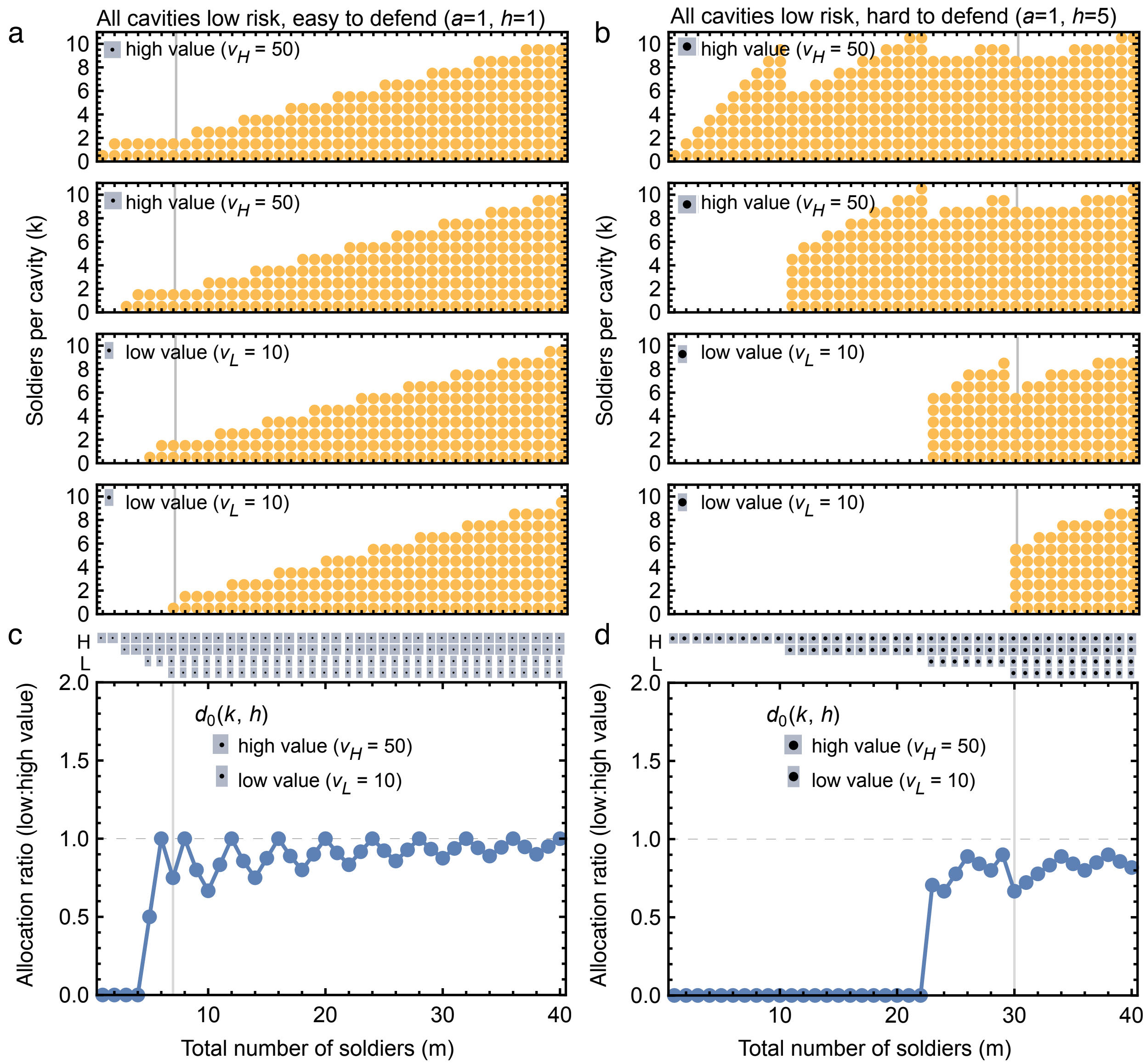

Figure 2

Numerical examples: optimal soldier deployment depending on asset value. (a) and (b) show the optimal way to divide m soldiers (x axis) into four available nest cavities (each represented by one vertically stacked panel: two of high value $v_H = 50$ and two of low value $v_L = 10$). Each yellow dot represents a single soldier. In (a) all cavities are easy to defend (small entrance, $h = 1$), while in (b), all cavities are hard to defend (large entrance, $h = 5$). (c) and (d) show the corresponding optimal allocation ratios, that is, the average number of soldiers per defended low-value cavity, divided by the average number of soldiers per defended high-value cavity. The dashed line represents a 1:1 ratio. Above each graph, grey nest icons indicate which cavities are defended by at least one soldier (have at least one yellow dot in the corresponding panel above). The vertical grey line indicates the asset-limited threshold, the minimum number of soldiers required for all four cavities to be defended. All cavities are subject to low risk (attack rate $a = 1$) and the defense model is the coverage model $d_0(k, h)$.

a 6:1 ratio (Figure 3c,d). Only under the diminishing-success model is the ratio affected by risk. When all cavities are at low risk of attack, the ratio initially peaks around 4.5:1, while under high risk the initial peak is at 4:1; in both cases, additional soldiers are added in a 5:1 ratio (Figure 3e,f). In this sense, the diminishing-success model induces a conservative response to risk: under higher risk of attack, the defensive skew towards the hard-to-defend cavities is reduced, with relatively more soldiers allocated to easy-to-defend cavities.

Risk of attack

When a colony is defense-limited, the optimal strategy may choose either low- or high-risk cavities to leave undefended. In most situations, it depends on the number of soldiers available (Figure 4a,b,c; see Supplementary Material Figure S4a,b,c,d,e). Initially, all soldiers are allocated to a low-risk cavity, but as the number of soldiers increases they are all shifted to a high-risk cavity while the low-risk cavity is left undefended. Only for the diminishing-success model with hard-to-defend cavities is the choice consistent: high-risk cavities are only defended if all low-risk cavities are also defended (Figure 4d). When a colony is asset-limited and cavities are easy to defend, the optimal strategy allocates approximately equal numbers of soldiers to low and high risk cavities regardless of the defense model (Figure 4a; see Supplementary Material Figure S4a,c,e). However, when a colony is asset-limited and cavities are hard to defend, risk impacts the optimal allocation ratio in different ways, depending on the defense model. With the coverage model and the accelerating-cost model, the optimal strategy allocates any extra soldiers to high-risk cavities (Figure 4b,c), but with the diminishing-success model, the optimal strategy allocates any extra soldiers to low-risk cavities (Figure 4d). Again, the diminishing-success model induces a conservative response to risk, in the sense that it prioritizes the defense of low-risk cavities, both in terms of asset choice under defense limitation and allocation ratio under asset limitation.

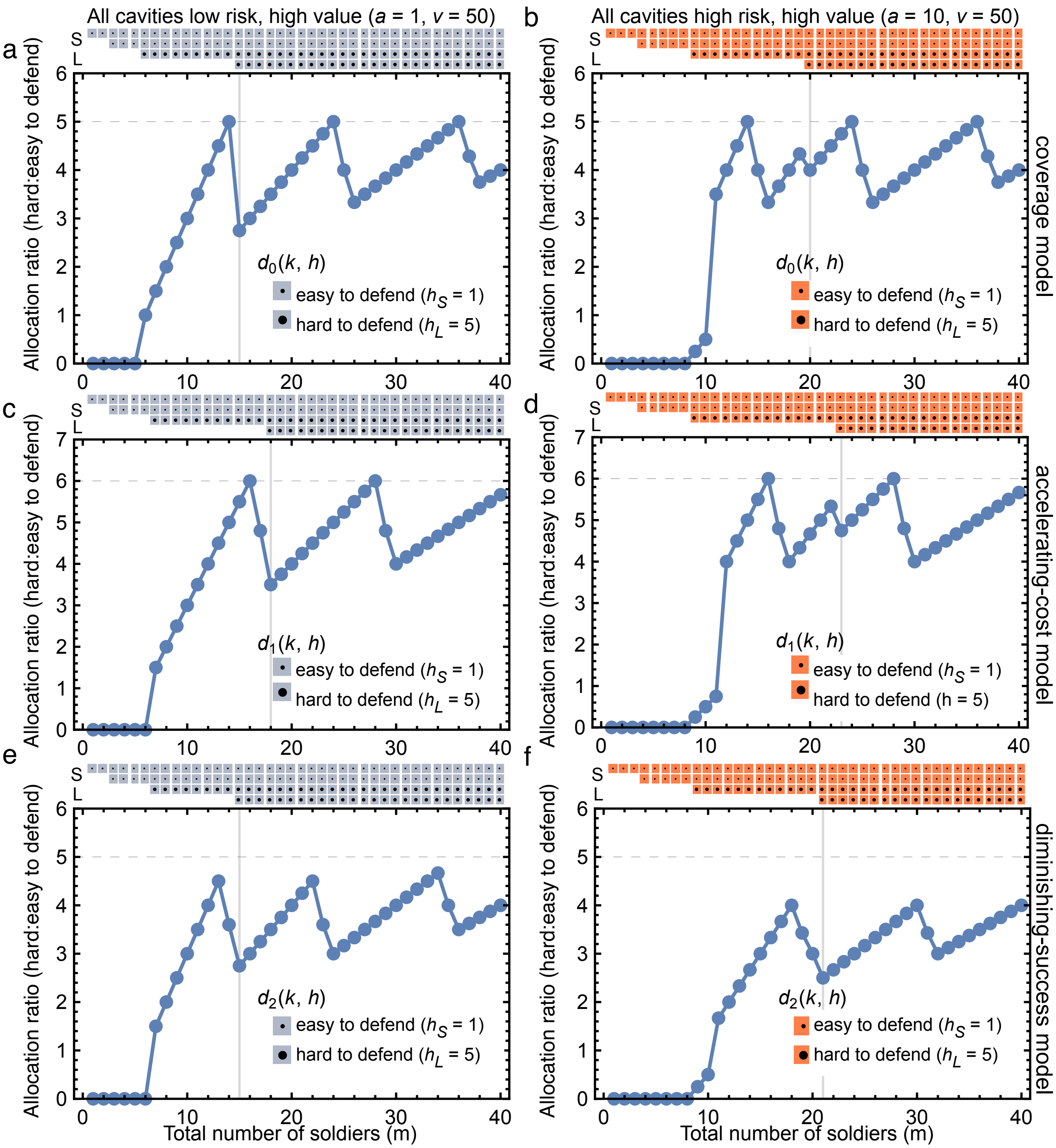

Figure 3
Numerical examples: optimal soldier deployment depending on defendability. Each graph shows the optimal allocation ratios for dividing soldiers among four available cavities, where two are easy to defend (small entrance, $h_S = 1$) and two are hard to defend (large entrance, $h_L = 5$). The ratio is calculated as the average number of soldiers in defended hard-to-defend cavities, divided by the average number of soldiers in defended easy-to-defend cavities. For (a, c, e), the risk of attack is low (attack rate $a = 1$); for (b, d, f) the risk of attack is high (attack rate $a = 10$). For (a, b) the optimal strategy is calculated using the coverage model of defensive success d_0; for (c, d) using the accelerating-cost model d_1; for (e, f) using the diminishing-success model d_2 (see Table 2 for values of other parameters).

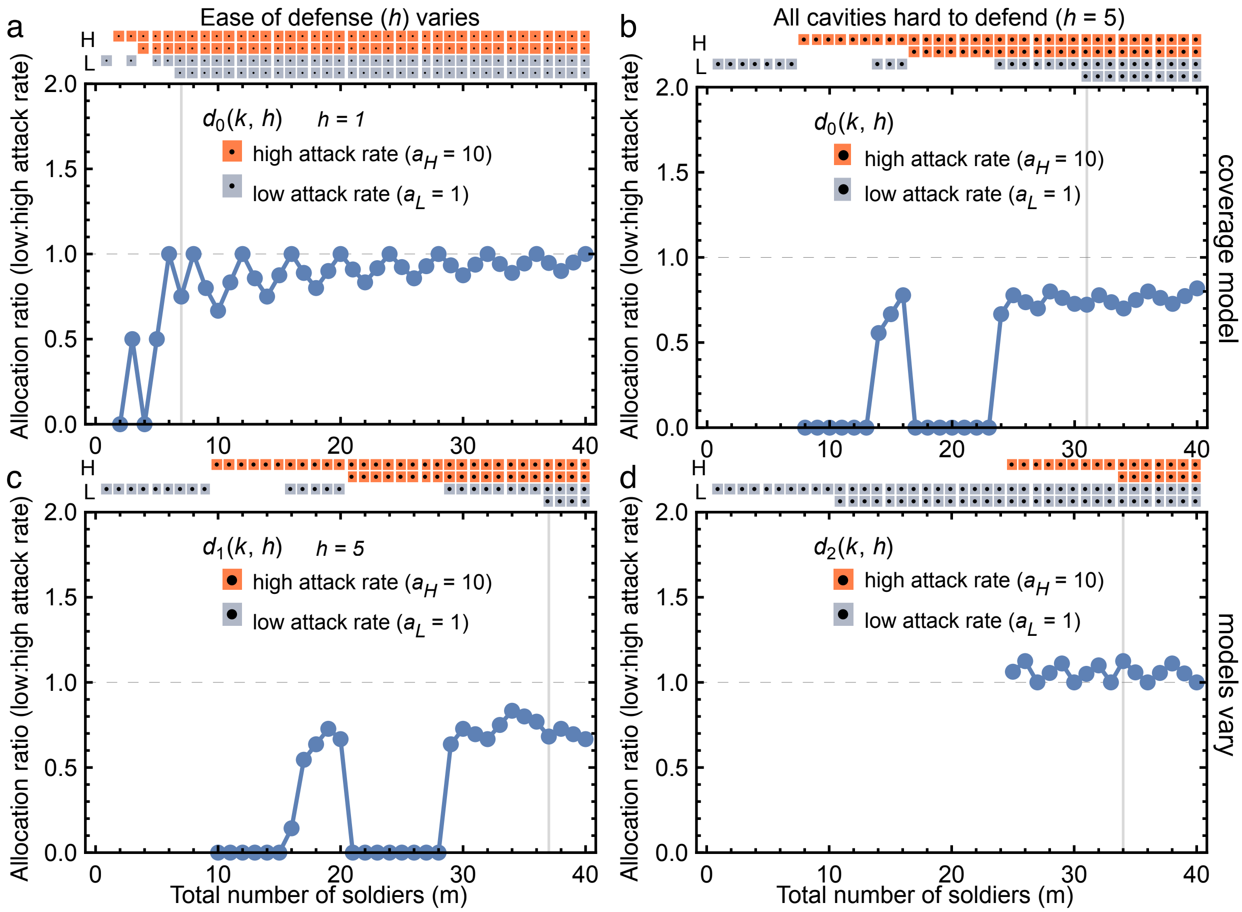

Figure 4
Numerical examples: optimal soldier deployment depending on risk of attack. Each graph shows the optimal allocation ratio for dividing soldiers among four available cavities, where two have high risk (attack rate $a_H = 10$) and two have low risk ($a_L = 1$). The allocation ratio is the average number of soldiers in defended low-risk cavities compared to soldiers in defended high-risk cavities. Note that the allocation ratio is undefined when no soldiers are in high-risk cavities. For (a), all cavities are easy to defend (entrance size $h = 1$); for (b, c, d) all cavities are hard to defend ($h = 5$). For panels (a, b) the optimal strategy is calculated using the coverage model of defensive success d_0; for panel (c) using the accelerating-cost model d_1; for panel (d) using the diminishing-success model d_2 (see Table 2 for values of other parameters).

Model analysis and generalization of results

The results of the numerical examples suggest a number of generalizations. Table 3 summarizes several features of the optimal strategy that are independent of the specific defense model, and result from more general assumptions of the model. Other features of the optimal strategy do depend on the defense model (see footnotes in Table 3); in particular, the diminishing-success model generates a uniquely conservative response to risk (specifically, footnotes b–d). Here, we will compare the marginal value curves for defenses at different types of assets across all three defense models, and argue that these results generalize beyond the specific numerical examples we chose.

Features common to the optimal strategy under all defense models

Below a certain threshold quantity of defenses, the optimal strategy is to concentrate defenses at just a few assets, rather than spreading them out among all assets. The advantage of aggregating defenses at a subset of assets is a consequence of the sigmoidal shape of the logistic family of defense functions (see Equation 1). Their sigmoidal form causes the marginal value curves for additional defenses to initially increase, rather than steadily decreasing, creating a peak in marginal value beyond a single defensive unit (see Figure 5). The marginal value curves show the fitness gained from allocating an additional defensive unit to a specific asset. Thus, until the peak in marginal value is reached, it is more valuable to add defenses to an asset that is already defended than to defend a new asset of the same type. The consolidation of defenses is most noticeable when individual assets require more defenses: when assets are difficult to defend (e.g. Figure 2b,d) and/or when risk of attack is high (e.g. Figure 3b,d,f). This occurs because the location of the peak in marginal value is shifted to the right for assets that are harder to defend (see Figure 5, blue vs. red curves) and when the risk of attack increases (see Figure 5b,d,f vs. 5a,c,e).

When limited defenses are consolidated into fewer assets, the optimal strategy involves

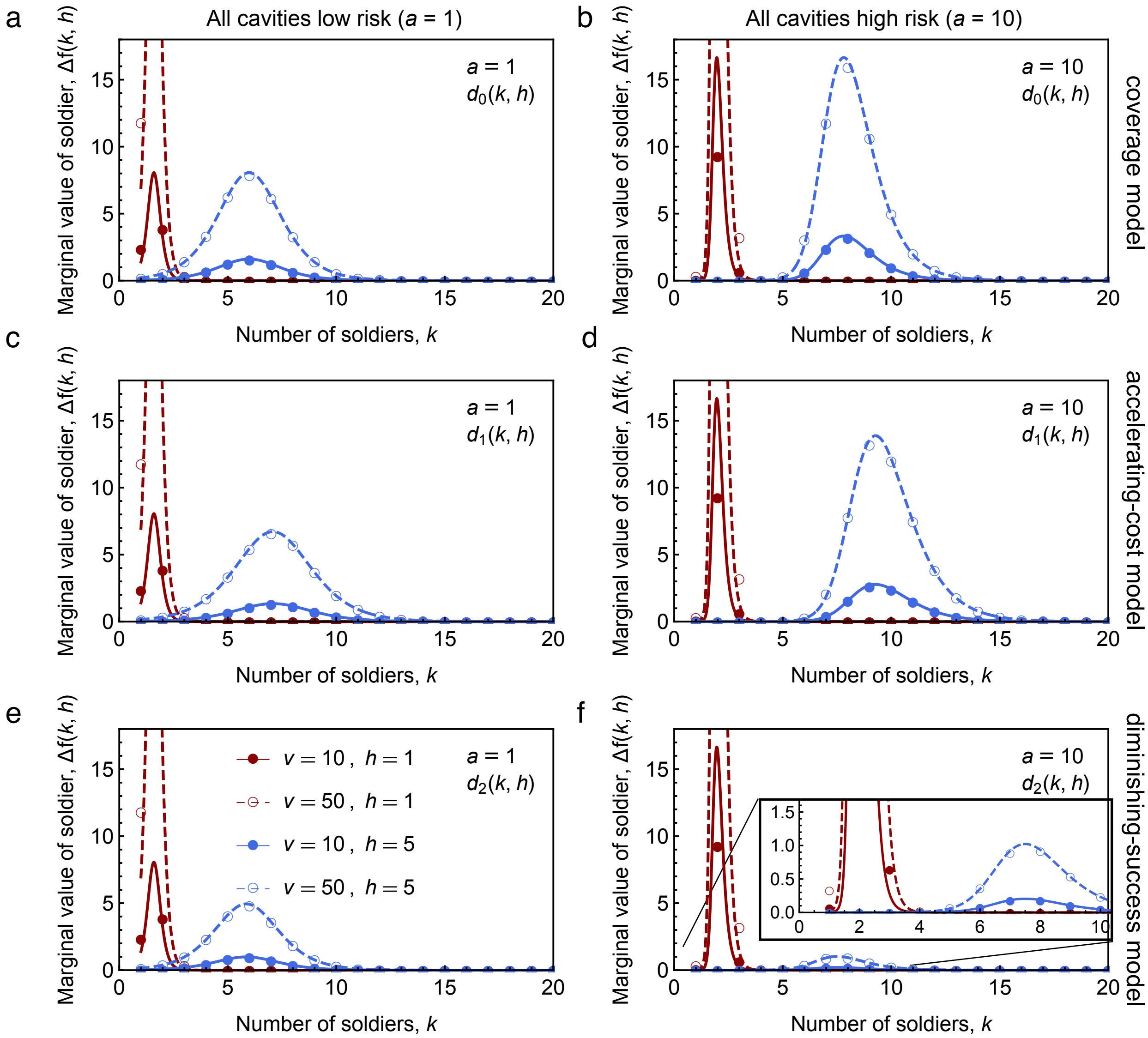

Figure 5
Marginal value of each soldier. The marginal value function $\Delta f(k, h, a, v)$ describes the contribution of one soldier to the colony's total potential reproductive fitness, if it is the kth soldier in a cavity with entrance size h, volume v, and risk of attack a. Within each panel, four marginal value curves are shown, for cavities with four different combinations of value and ease of defense (see legend in panel e). Panels on the left side (a, c, e) show the marginal values for low risk ($a = 1$) while panels on the right (b, d, f) show marginal values for high risk ($a = 10$). Panels in the top row (a, b) show marginal values for the coverage model d_0; panels in the middle row (c, d) show marginal values for the accelerating-cost model d_1; panels in the bottom row (e, f) show marginal values for the diminishing-success model d_2 (see Table 2 for values of other parameters).

a choice of which assets to defend: regardless of the model, it is always better to leave low-value or hard-to-defend assets undefended. High-value assets are chosen first because they contribute to fitness in proportion to their value (see Equation 6). Comparing the marginal value curves for high-value and low-value assets with the same ease of defense, we see that the kth defensive unit in a high-value asset contributes more to fitness than the kth defensive unit in a low-value asset (compare dashed to solid lines in Figure 5). Easy-to-defend assets are chosen first because we assume they require fewer defenses to defend them well, and each defensive unit contributes more to defense. That is, in all three defense models, as assets become harder to defend (h increases), the midpoint M increases and the steepness S decreases (Figure 1). Because the marginal value curves are related to the slope of the fitness gain for each asset as the number of defensive units allocated to it increases, the steepness of the defense function affects the height of the peak in marginal value, while the midpoint of the defense curve (the point of greatest steepness) affects its location. Thus, the peak in marginal value for hard-to-defend assets occurs with more defensive units and is lower than the peak for easy-to-defend assets (compare blue to red lines in Figure 5). Thus, in the defense-limited condition, all else being equal, a group can always gain more from defending an easy-to-defend asset than a hard-to-defend asset—just as it can gain more from defending a high-value asset than a low-value asset.

When assets are limiting, instead, the optimal strategy balances defenses across assets in a way that depends strongly on defendability, but less strongly on either value or risk of attack. In the numerical examples, we saw that assets with a 5-fold difference in value were defended in approximately a 1:1 ratio (Figure 2), as are assets with a 10-fold difference in risk (Figure 4). In contrast, assets with a 5-fold difference in perimeter size were defended at a ratio of 4:1 to 6:1, depending on the model. This ratio is governed by two features: (1) the relative location of the peaks in marginal value, which determine the optimal allocation ratio at the transition from an asset-limited to a defense-limited state, and (2) the relative rate at which the marginal value curves decay, which determines the optimal ratio at which extra defenses beyond that threshold are placed at each asset. For each asset, the location of the peak in marginal value is strongly determined by ease of defense (compare red to blue lines in Figure 5), weakly affected by risk (compare Figure 5a,c,e to 5b,d,f), but not affected by asset value at all (compare dashed to solid lines in Figure 5.) Furthermore, the rate at which the marginal value curves decay converges quickly to a constant which depends only on asset defendability (perimeter size h and the defense model $d(k, h)$), but not on asset value or on the risk of attack (see Supplementary Material S2).

Unique features of the optimal strategy under the diminishing-success model

Under the diminishing-success model, it is optimal to prioritize defense of low-risk assets when defenses are limited, a conservative response to risk that does not occur in the other two models. The numerical examples for risk of attack show that, for the coverage model and the accelerating-cost model, depending on the degree of defense limitation, it may be advantageous for a group to defend a high-risk asset instead of a low-risk asset; in contrast, for the diminishing-success model the low-risk assets always take priority (see Figure 4). In the first two models, the effect of risk is to shift the peak in marginal value to the right and up, so that assets under higher risk of attack require more defenses to defend them well, but the value of each defensive unit is higher (compare Figure 5a,c to 5b,d). This means that the optimal choice depends on the number of defensive units available: it is advantageous to choose to defend high-risk assets, but only if there are sufficient defensive units to do so well. In contrast, under the diminishing-success model, the effect of risk is to shift the peak in marginal value to the right, and for assets that are hard to defend, also down (compare Figure 5f to 5e). This is because, under the diminishing-success model, hard-to-defend assets can never be defended as well as easy-to-defend assets, even with maximal defense. As a result, when assets are difficult to defend, high-risk assets both require more defensive units to defend them, and are less worth defending.

When assets are limiting, risk of attack affects the optimal balance of defenses across assets that differ in perimeter size for the diminishing-success model, but not for the other two models. The numerical examples for asset defendability show that under the diminishing-success model, increased overall risk of attack shifts the optimal allocation ratio away from hard-to-defend assets (compare Figure 3f to 3e), but has no impact on optimal allocation ratio for the other models (compare Figure 3b to 3a and 3d to 3c). This occurs because in the coverage and accelerating-cost models, higher risk of attack increases the height of the peaks in marginal value in the same way, regardless of perimeter size, so the relative peak heights stay the same (compare Figure 5b to 5a and 5d to 5c). In contrast, in the diminishing-success model, the impact of risk on the peak heights depends on asset perimeter size: higher risk actually reduces peak height, but only at hard-to-defend assets (compare Figure 5f to 5e). This striking difference in the impact of risk is a result of the fact that, under the assumptions of the diminishing-success model, even well-defended hard-to-defend assets are likely to succumb to attack and are thus less worth defending than easy-to-defend assets.

Although the optimal strategy is to allocate defenses approximately equally across assets regardless of risk, under the diminishing-success model low-risk assets get any additional defenses, while under the other models the high-risk assets get any additional defenses. Increasing risk of attack shifts the peaks in marginal value to the right for all models (compare Figure 5b to 5a, 5d to 5c, and 5f to 5e). For the coverage model and the accelerating-cost model, risk of attack also increases the height of the peak (compare Figure 5b to 5a, and 5d to 5c). Together, these two things mean that for those two models the optimal strategy is to prioritize defense at assets that are under higher risk of attack. However, for hard-to-defend assets under the diminishing-success model, the optimal strategy is to prioritize defense at assets under low risk of attack, because increased risk of attack reduces the height of the peak (compare blue curves in Figure 5f to 5e). The reason that hard-to-defend, high-risk assets are avoided only for the diminishing-success model is that, under its assumptions, hard-to-defend assets that are under higher risk of attack have more opportunity for defenses to fail even when well defended, making them less worth defending.

Discussion

In this article, we have developed a mathematical model of defense that focuses on the adaptive deployment of defenses: what is the optimal way to distribute limited defenses among multiple assets, depending on their value, defendability and risk of attack? We focus in particular on the impact of asset defendability, comparing three versions of the model that make different assumptions about how assets vary in the costs of defense and/or the chance of successful defense. We derive from all three models that it is critical to distinguish between a defense-limited and an asset-limited state; in other words, between the decision of which assets to defend at all when defenses are limited, and how much defense to allocate to each asset when defenses are plentiful. Across all three models, we find that in the defense-limited state, the optimal strategy is to focus defensive effort on high-value, easy-to-defend assets while abandoning low-value or hard-to-defend assets. In the asset-limited state, defendability has a stronger impact on the optimal defensive allocation than either value or risk of attack, with far more defensive effort being allocated to the assets that are most difficult to defend. Beyond these commonalities, however, for just one of the three models of defendability—the diminishing-success model, in which even formidable defenses are likely to fail—we find that a conservative response to risk is optimal. That is, under some conditions it may be favorable to accept a high chance of defeat and to instead conservatively consolidate defenses at assets that have a higher chance of being successfully defended: those that are easy to defend and/or at low risk of attack.

The feature of asset choice—the fact that, for all three models, the optimal strategy aggregates limited defenses at a subset of assets—is not an inevitable consequence of any defense model, but rather a result of the general family of defense functions we chose. Such consolidation of defenses has in fact been observed in laboratory experiments with the turtle ant *Cephalotes rohweri*: under conditions of higher risk, colonies defended fewer cavities, and concentrated defenses primarily in well-established nests (Powell et al., 2017). This trade-off between defending a few assets well and defending many poorly is analogous to the well-established tradeoff between size and number of offspring. Many organisms are capable of shifting between life-history strategies, producing either a few large offspring with high fitness or many small offspring with lower fitness. Often, the optimal offspring size changes depending on environmental conditions, typically increasing under harsher conditions where offspring survival is lower (Smith and Fretwell, 1974; McGinley et al., 1987; Einum and Fleming, 2004; Hassall et al., 2006). Similarly, we find that under higher risk of attack, the optimal defensive strategy is to concentrate more defenses at fewer assets. The similarity is due to the general shape of the investment/benefit curves: in both cases, benefits (chance of survival or successful defense) initially increase slowly for small investment (in offspring size or asset defense), then increase rapidly, and finally plateau. Under harsher environmental conditions, small offspring are unlikely to survive and thus are not worth producing; similarly, under high risk of attack, poorly defended assets are unlikely to be retained, and so are not worth defending. The consolidation of defenses into fewer assets under risk might be a strategy shared by other organisms, which, if observed, could suggest a sigmoid defense curve.

By separating each strategy into the two components of asset choice and relative allocation of defenses, we see that value and defendability influence these two components in qualitatively different ways, regardless of which of the three defense models is used. For value, the optimal strategy is to choose to defend higher-value assets when defenses are in limited supply, and to allocate any extra defenses to those same assets when defenses are plentiful. In contrast, for defendability, the optimal strategy is to prioritize easy-to-defend assets when defenses are scarce, but to concentrate defenses at hard-to-defend assets when defense availability is high. Considering these two aspects together highlights a potential tension between the choice of which assets to defend and the optimal level of investment in those assets, which holds regardless of specific assumptions about how defendability varies across assets. Intuitively, it might seem that what is worth defending at all should be worth defending well. For value, this intuition holds: the optimal strategy is to defend high-value assets, and invest more in their defense. However, when it comes to defendability, the assets that are most worth defending are actually those requiring the least amount of defensive effort. In fact, the reason it is optimal to choose those assets is precisely because they require less defensive investment to achieve the same levels of defensive success.

The tension between the choice to defend an asset at all and the quantity of defensive resources to allocate to it raises an interesting question: how might a distributed decision-making entity, such as a social insect colony, actually implement an optimal deployment strategy? Such a colony faces conflicting objectives, depending on the conditions: to preferentially defend easy-to-defend assets when the colony is defense-limited, but to allocate more defenses to hard-to-defend assets when the colony is asset-limited. It is difficult to see how individual preferences based on defendability alone could produce such behavior. There may be simple rules of thumb that individual soldiers could follow, where preference is modulated for example by the presence of other soldiers in a cavity. This might yield adaptive group behavior most of the time, as seen for example in models of social insect foraging (Camazine and Sneyd, 1991; Hirsh and Gordon, 2001; Detrain and Deneubourg, 2008). Intriguingly, laboratory experiments with *C. rohweri* showed that while colonies did allocate more soldiers to cavities that are difficult to defend, they did not choose to defend easy-to-defend cavities over hard-to-defend ones—even though such cavities showed much higher survival in the field (Powell et al., 2017). This observation stands in contrast to field experiments with *C. persimilis*, in which artificial cavities with smaller entrances were chosen and defended (Powell, 2009). Examining how individual decisions lead to group-level patterns of occupation and defense under different conditions for these different species, empirically and theoretically, might explain why such different group behaviors are observed.

Although the qualitative results for all three defense models are similar in many ways, the assumptions of the diminishing-success model in particular generate more conservative optimal strategies which invest preferentially in defending low-risk, easy-to-defend assets. Comparing the optimal defense strategies generated by these models with empirical results from laboratory experiments in turtle ants, we find that the lower rate of successful defense in the diminishing-success model can explain a surprising feature of the turtle ants' defensive deployment strategy. Under conditions of elevated risk, colonies of *C. rohweri* responded by reducing defenses at the most difficult-to-defend cavities (Powell et al., 2017), a counter-intuitive result which seemed at odds with general models of colony task allocation (e.g. Cornejo et al., 2014). However, reduced investment in high-risk assets under risk is a unique prediction of the diminishing-success defense model, arising from its biologically-inspired assumption that some cavities are more difficult to defend, not just because they require more investment to defend well, but also because the nature of the interactions means it is likely that even well-defended cavities will succumb to attack. This assumption fits the ecology of turtle ants with highly specialized defensive soldiers, because soldiers create a physical blockade with their armored heads, and in larger entrances, those physical blockades are less structurally sound (Powell, 2008). Variation between cavities in the likelihood that an attack will be successful may thus explain why *C. rohweri* colonies take a conservative, risk-limiting approach to defensive deployment. The diminishing-success model also predicts, again counter-intuitively, that colonies should invest fewer soldiers in defending cavities that are more likely to be attacked, for example because they are more accessible to competitors. Future empirical studies could examine how soldier deployment responds to variation in risk of attack among nests, to explore whether turtle ant colonies indeed invest less in threatened assets in order to limit risk. Other species in the large and diverse *Cephalotes* genus have soldiers that are less specialized in defense (Powell, 2008, 2016; Powell et al., 2020), presenting the opportunity for a comparative study of the turtle ants examining the relationship between defensive morphology, the effects of entrance size and soldier number on defensive success, and the defensive strategy in response to risk (see Supplementary Material S1).

We developed here a general model of defensive allocation, inspired by polydomous ant colonies, but with potential applications in plant defense, resource defense, and other systems where limited defenses must be divided among multiple assets. By bringing together aspects of prior work in optimal plant defense theory and resource defense theory, augmented with insights from the study of collective behavior in social insects, we make two important conceptual additions which could broaden the scope of such models to other organisms or groups allocating limited defenses among multiple assets. First of all, we show that differences among assets in defendability can have even stronger impacts on defensive allocation than differences in value or risk of attack. Prior work on the allocation of chemical defenses across leaves has suggested that younger leaves are better protected because they are more valuable to the plant (van Dam et al., 1996) or at higher risk of attack (Zangerl and Rutledge, 1996). However, younger leaves may also be better protected because they are harder to defend: if leaves increase in toughness as they age, they may need less concentrated chemical defenses to produce the same aversive effect on herbivores (Brunt et al., 2006; Mason and Donovan, 2015). For animals that defend multiple food resources, such as ant colonies defending trees with aphid colonies, defendability might depend not just on the perimeter size of the food resource but also how competitors would access it (Hölldobler, 1979), suggesting an interesting comparison between defensive strategies for ants based on whether their primary competitors travel on the ground or via connecting branches in the canopy (Jackson, 1984; Tanner, 2008). Second, we compare two different ways in which certain assets can be disproportionately hard to defend: they require increasingly more defense, or the likelihood of defensive failure grows. While plant defense theory has generally focused on the costs of defense, the chance of defensive success may also vary across plant tissues: for example, the use of nectaries to recruit ant defenders has been suggested to be more effective at cotton leaves than at fruits, because herbivores are more accessible to the ant defenders on the leaves than they are within the fruits (Wäckers and Bonifay, 2004). For ant colonies, the chance of successfully defending a food resource may depend on the size and nature of the food source, which affects the types of competitors attracted to it (Kaspari, 1993; Blüthgen and Fiedler, 2004; Adler et al., 2007). Variation in these two aspects of defendability—defense costs and the chance of successful defense—generate optimal strategies with qualitatively different responses to risk. This suggests that different organisms in different contexts will respond defensively to increased risk in different ways, but that by characterizing not just whether but also how assets differ in defendability, we may be able to qualitatively predict whether defensive allocation is sensitive to risk and in what way.

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Statement of Authorship

M.D.-M. conceptualized the model with feedback from S.P. and A.D., and M.D.-M. implemented and analyzed the model. All authors contributed to writing, reviewing and editing the manuscript.

Data and Code Accessibility

A Mathematica notebook containing code for the model, analysis, and all figures is available on Zenodo with DOI 10.5281/zenodo.5757571.

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