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Foraging Challenges: Unsuitable Prey and Limited Information

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FORAGING CHALLENGES: UNSUITABLE PREY AND LIMITED INFORMATION

by

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FORAGING CHALLENGES: UNSUITABLE PREY AND LIMITED INFORMATION

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Food acquisition is a complicated task. The profitability of potential food items depends on numerous factors, including the spatial distribution, probability of detection and capture, and suitability of the food. Animals faced with such challenges can use relatively simple mechanisms to maximize foraging efficiency. However, mechanisms that maximize foraging efficiency under some ecological conditions (e.g., prey scarcity) may produce ostensibly suboptimal behavior under different ecological conditions (e.g., prey abundance). In the work presented here, we explore two facets of foraging: (1) consuming unsuitable prey, and (2) searching for resources with limited information about resource location.

To explore the consequences of consuming unsuitable prey on predator behavior, we first measured the suitability of two aphid species, black bean aphids and pea aphids, for a native predatory insect, the convergent ladybird beetle. Ladybird larvae had lower larval survival, longer developmental times, and lower adult weights on a diet of bean than pea aphids. We found that ladybird larvae killed bean aphids even if pea aphids were abundant, presumably because bean aphids were easier to capture than the pea aphids. Consumption of even a single bean aphid had pronounced short-term (< 1 day) effects on predator behavior. Ladybird larvae had longer handling times, longer bouts of inactivity, shorter bouts of intensive search, and lower patch-leaving tendencies after eating a bean aphid than after eating a pea aphid. The general

lethargy from eating bean aphids may reduce the foraging efficiency of ladybird larvae.

We built a simulation model to explore the performance of composite search strategies on landscapes where resource distributions ranged from dispersed to clumped. The search strategies involved switching between intensive and extensive modes based on either resource encounters or sensory cues. We found that the search strategy based on sensory cues outperformed the search strategy based on resource encounters across all resource distributions and was more robust to changes in the resource distribution.

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Chapter 1

Larval performance and killing rate of convergent ladybird beetles on black bean aphids and pea aphids

1.1 Abstract

Generalist predator guilds play a prominent role in structuring insect communities and can contribute to limiting population sizes of insect pest species. A consequence of dietary breadth, particularly in predatory insects, is the inclusion of unsuitable, or even toxic, prey items in the predators diet. Consumption of unsuitable prey items reduces growth, development, and survival of predator larvae. The objective of this paper was to examine the effect of a suspected unsuitable aphid species, black bean aphids (*Aphis fabae*), on the larval performance of an abundant native predator species, convergent ladybird beetles (*Hippodamia convergens*), in North America. For comparison, ladybird larvae were also reared on a known suitable aphid species, pea aphids (*Acyrthosiphon pisum*), and on a 50:50 mix of both aphid species. Survival of

ladybird larvae reared on the bean aphid diet was dramatically lower (0.13) than on the pea aphid diet (0.70), and survival on the mixed diet was intermediate (0.45) to survival on the single-species diets. Surviving ladybird larvae developed more slowly and weighed less as adults on the bean aphid diet than on the pea aphid diet. Despite the relatively poor performance on the bean aphid diet, ladybird larvae killed large numbers of bean aphids. Furthermore, ladybird larvae killed more bean aphids than pea aphids in the mixed diet treatment, most likely because bean aphids were easier to catch than pea aphids. Our results suggest that the continued spread of bean aphids in North America might pose a considerable foraging challenge for convergent ladybird beetles.

1.2 Introduction

Generalist predators play a prominent role in structuring insect communities through intraguild predation [40], apparent competition [48], and tritrophic interactions [10]. The numerous potential interactions that involve generalist predators complicate predictions about when generalist predator guilds can contribute to limiting insect pest populations [30, 49], which has produced a contentious debate about the overall effectiveness of generalist predators in biological control [22, 45]. One factor that can complicate predictions about the effectiveness of top-down control by generalist predators is the co-occurrence of multiple potential prey species [17, 24, 35], particularly if species in the prey community vary in suitability [48], encounter probability [1], or capture probability [36].

Ladybird beetles are prominent generalist predators in insect communities and widely used as biocontrol agents [30, 31, 49]. The primary prey of aphidophagous ladybird beetles vary widely in both suitability [27] and vulnerability [26]. The assessment of prey suitability for ladybird beetles typically involves measuring predator performance in laboratory feeding trials rather than direct measurement of the energy content, nutrient composition, or toxic compounds of the prey. For the larval stage, prey species that support development to the adult stage are considered suitable prey with the degree of suitability dependent on the developmental rate and/or adult mass [27]. Toxicity may be inferred indirectly through very low larval survival and sublethal effects on predator behavior (see Chapter 2).

Consumption of unsuitable prey is particularly likely when suitable prey are scarce because generalist predators respond to the threat of starvation by including unsuitable prey items in their diet [7, 41, 43]. Even when suitable prey are abundant, the availability of suitable prey to predators may be depressed if they are difficult to catch and subdue [25, 36]. For toxic prey, there is often a trade-off between chemical defense and alternative defense mechanisms [33], suggesting that predators can capture toxic prey more easily than suitable prey. As a consequence, the vulnerability of prey to predation often plays a more prominent role in predators' diet selection than the nutritional quality or toxicity of prey [42].

Black bean aphids (*Aphis fabae*) are a polyphagous cosmopolitan pest [6] that varies widely in suitability as food for ladybird beetles (Table 1.1). However, the suitability of bean aphids as a food for one of the most abundant native ladybird beetles in North America, convergent ladybird beetles (*Hippodamia convergens*), is unknown. Bean aphids were introduced to North America about 130 years ago and have achieved pest status [13]. In general, ladybird beetles show little selectivity among prey types and even consume toxic prey in laboratory studies [3, 12, 28, 29]. Thus, convergent ladybird beetles may pay steep fitness costs associated with the inability to avoid consuming bean aphids.

Our central objective was to measure the larval performance of convergent ladybird

Table 1.1: Literature survey of survival to the adult stage for several species of ladybird beetle larvae when reared on a diet of black bean aphids.

Ladybird species	Survival	Host plant	Source
Adalia bipuncata	0.33	*Atriplex sagittata*	[20]
Coccinella undecimpunctata	0.50	*Vicia faba*	[4]
Hippodamia variegata	0.66	*Vicia faba*	[11]
Adalia bipuncata	0.67	*Philadelphus coronarius*	[20]
Cycloneda sanguinea	0.81	*Vicia faba*	[19]
Ceratomegilla undecimnotata	0.89	*Vicia faba*	[23]
Coccinella septempunctata	0.93	*Vicia faba*	[23]
Coccinella septempunctata	0.93	*Atriplex sagittata*	[21]
Coccinella septempunctata	0.93	*Philadelphus coronarius*	[21]
Propylea quatuordecimpunctata	0.96	*Vicia faba*	[23]

beetles on a diet of bean aphids. For comparison, ladybird larval performance was also measured on a diet of pea aphids (*Acyrthosiphon pisum*), which is a suitable food for a large number of coccinellid species [21, 39, 46], including convergent ladybird beetles [16]. Pea aphids were introduced to North America at roughly the same time as bean aphids [13], overlap in a set of suitable host plants with bean aphids [47], and readily colonize broad bean plants containing bean aphids in the laboratory (Hinkelman and Tenhumberg, unpublished data). The presence of multiple prey species on a plant (or in a field) can alter the top-down effects of a generalist predator via changes in prey selection and predator performance [10, 17]. Thus, prey selection and performance of ladybird larvae were examined on a diet comprised of both aphid species. Laboratory tests of prey selection provide a baseline test of the potential negative effects of unsuitable prey on generalist predators.

1.3 Methods

Pea aphids and bean aphids were maintained in separate cultures with broad beans as the host plant. Adult convergent ladybird beetles were housed in cages with pea aphids and broad beans. Adult convergent ladybird beetles were purchased from a commercial supplier (A-1 Unique Insect Control, Citrus Heights, California, USA), which collects ladybird beetles from the Sierra Nevada Mountains and maintains them in dormant state through cold storage (3°C). In the laboratory, all insects were reared at approximately 24°C on a 16:8 hour photoperiod. To avoid egg cannibalism, eggs were removed from the ladybird beetle culture and placed in a separate cage for hatching. Recently hatched ($<$ 24 hrs) ladybird larvae were placed individually in plastic vials (26x67 mm) and randomly assigned to one of three diet treatments: (1) bean aphids only, (2) pea aphids only, and (3) 50:50 mix of bean and pea aphids.

Each day the live and dead aphids remaining in each predators vial were counted and removed. Dead aphids were divided into two categories: those that showed evidence of piercing by the mouthparts of ladybird larvae (killed) and those with no evidence of piercing (dead). The number of aphids killed each day was determined by subtracting the number of live and dead aphids from the number of aphids supplied the previous day. Ladybird larvae were provided with fresh aphids daily. The number of aphids fed each day was based on the number of aphids killed on the previous day. Thus, feeding was tailored to each individual ladybird larvae and did not follow a set schedule. Across all three treatments, aphids were subjectively (by eye) size matched by selecting large bean aphids and similarly-sized pea aphids to ensure that differences in preference or performance were not attributable to aphid size differences because apterous pea aphid adults ($\approx$ 3.8 mg) are 4x larger than apterous bean aphid adults ($\approx$ 0.9 mg) [8].

Three measures of ladybird larval performance were examined: (1) larval survival (binary response), (2) developmental time to the adult stage (days), and (3) adult mass (mg). Adult mass was used as an indicator of fecundity because adult size is positively correlated with reproductive capacity [44]. The relationship between diet treatment and performance variables was analyzed with either a generalized linear model with a binomial error distribution (survival) or linear models with normal error distributions (developmental time, mass). The overall effect of the diet treatment on each performance variable was tested with either analysis of deviance (survival) or analysis of variance (developmental time, mass).

Locally weighted polynomial regression models were fit separately for each diet treatment to characterize the relationship between the number of aphids killed each day and the age of the ladybird larvae. The data were split into two subsets based on whether or not the ladybird larvae survived to the adult stage because the number of aphids killed at a given age was related to the developmental stage of the ladybird larvae and unsuccessful ladybird larvae typically developed more slowly than successful ladybird larvae.

For ladybird larvae on the mixed diet, prey selection was tested with a two-tailed sign test by comparing the total number of each aphid species consumed over the duration of the larval period. Significant selectivity, therefore, indicates that the two aphid species were not consumed in the same proportion as available in the environment [42]. R was used to conduct all statistical analyses [38].

1.4 Results

The diet treatment significantly affected all three performance measures for ladybird larvae (larval survival: $\text{deviance}_{2,86} = 21.4, p < 0.001$; developmental time: $F_{2,35} =$

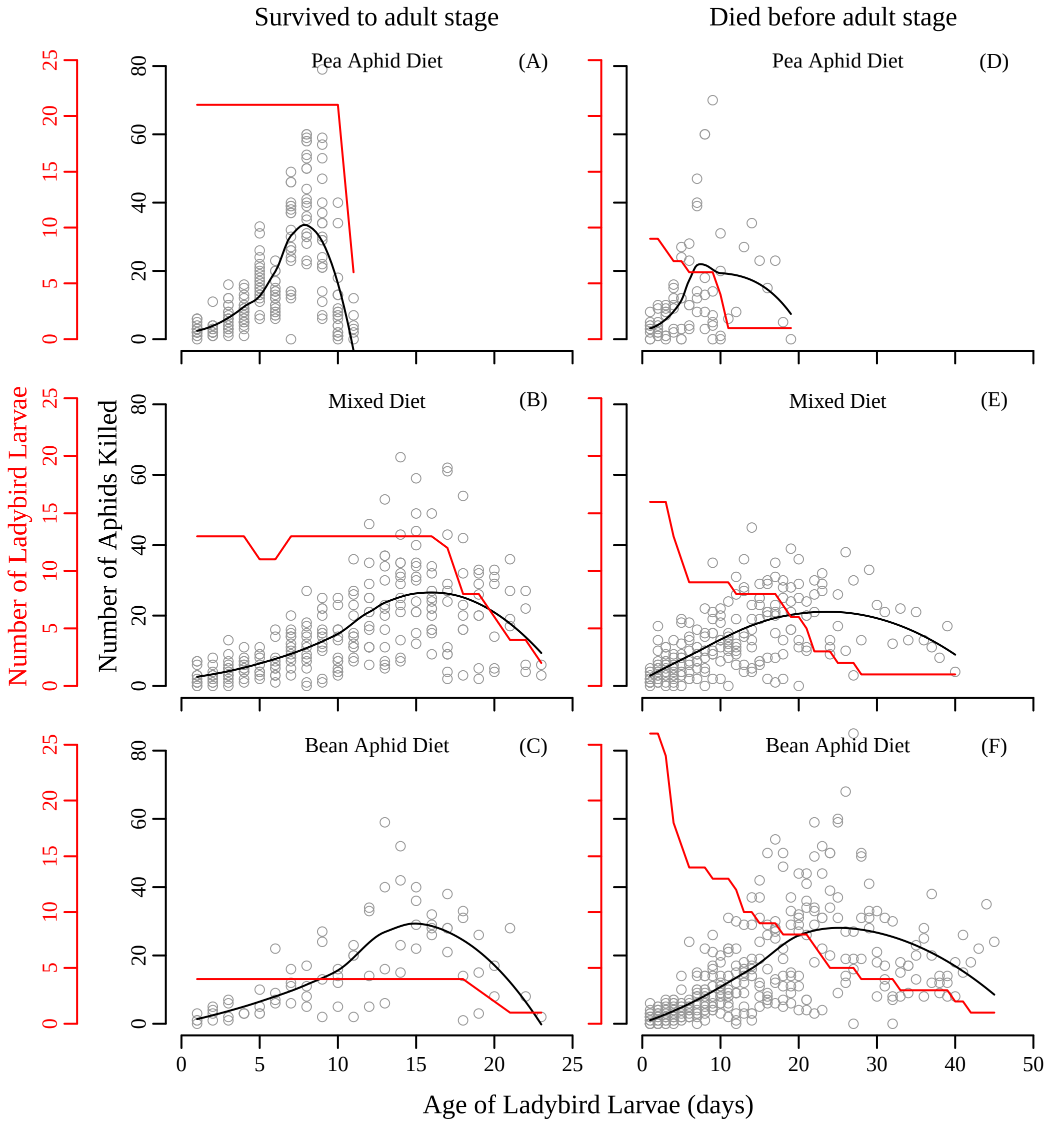

Figure 1.1: Number of aphids killed each day by ladybird larvae on three diet treatments: bean aphids alone, pea aphids alone, and 50:50 mix of bean and pea aphids. Black lines are locally weighted polynomial regression models of aphids killed each day. Data was divided based on the fate of the ladybird larvae. [Note the different range of the x-axis for (A-C) and (D-F).] Red lines indicate the number of ladybird larvae receiving food each day. The early dip in the red line in (B) arises from missing data because of a data recording error rather than the pupation or death of ladybird larvae.

Table 1.2: Performance of ladybird larvae on three diet treatments: black bean aphids alone, pea aphids alone, and 50:50 mix of bean and pea aphids. Values presented are the predicted mean ± standard error from the statistical models. Values followed by different letters are significantly different. Estimates for developmental time and mass include only larvae that survived to the adult stage.

Diet	Larval Survival[1]	Developmental Time (days)[2]	Adult Mass (mg)[2]
Bean aphid	0.13±0.06 a	26.3±0.8 a	10.9±1.6 a
Mixed	0.45±0.09 b	26.3±0.5 a	12.1±0.9 a
Pea aphid	0.70±0.08 c	17.0±0.4 b	21.5±0.7 b

[1] Sample size: Bean aphid – 30, Mixed – 29, Pea aphid – 30
[2] Sample size: Bean aphid – 4, Mixed – 13, Pea aphid – 21

$139.9, p < 0.001$; adult mass: $F_{2,35} = 45.9, p < 0.001$). Survival was significantly higher on a diet comprised of pea aphids (0.70) than bean aphids (0.13); survival on the mixed diet (0.45) was intermediate to survival on the diets of single aphid species (Table 1.2). Developmental time to the adult stage was significantly shorter, and adult mass was significantly greater, on the pea aphid diet than on either of the other two diets (Table 1.2). The number of aphids killed by ladybird larvae peaked earlier, and more sharply, on the pea aphid diet than on either of the other two diets (Figs. 1.1). Although ladybird larvae performed better when fed pea aphids, ladybird larvae on the mixed diet killed significantly fewer pea aphids than bean aphids over the duration of the larval period ($p = 0.024$; Fig. 1.2).

1.5 Discussion

The objective of this study was to examine the fitness consequences of consuming the insect pest, black bean aphids, on a native predatory insect in North America, convergent ladybird beetles. Our results suggest that bean aphids are an unsuitable prey that significantly influenced three measures of ladybird larval performance. A

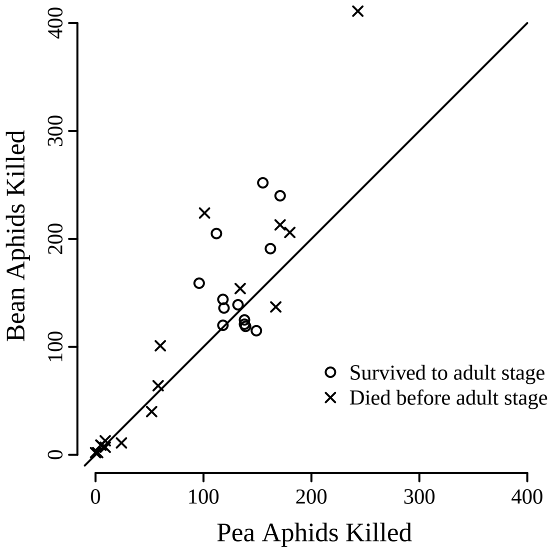

Figure 1.2: Total number of aphids killed over the duration of the ladybird larval period on a 50:50 mixed diet of pea aphids and bean aphids. Symbols indicate fate of ladybird larvae. Reference line indicates no difference in number of bean and pea aphids killed.

bean aphid diet increased developmental time and reduced survival and adult mass of ladybird larvae relative to a diet of pea aphids. Consuming bean aphids increased the developmental time of ladybird larvae resulting in a delay in peak killing capacity relative to the pea aphid diet. Ladybird larvae took a very long time to pupate or die on the bean aphid diet (Fig. 1.1C & 1.1F) and, as a consequence, they killed as many aphids on the bean aphid diet (202 ± 37 aphids/larva) as larvae on the pea aphid diet (148 ± 31 aphids/larva) over their entire larval periods (generalized linear model, $t = -1.12, df = 58, p = 0.27$). Our findings are not limited to bean aphids grown on broad beans; using sugar beets (*Beta vulgaris*) as a host plant produced a similarly negative effect for convergent ladybird larvae (Tenhumberg, unpublished data). To our knowledge, larval survival on a bean aphid diet is lower for convergent ladybird larvae than any other ladybird beetle species previously tested (Table 1.1). Although compounds sequestered from host plants can contribute to aphid defense [34], there is no clear effect of host plant on suitability of bean aphids for ladybird beetles (Table 1.1).

The poor performance on diets that include bean aphids in this study is unlikely to be caused by prey limitation because excess aphids were provided daily and convergent ladybird larvae rarely fully consume bean aphids (Chapter 2). Partial consumption of bean aphids has also been reported for the two-spotted ladybird beetle (*Adalia bipunctata*) [3]. Furthermore, behavioral experiments show that convergent ladybird larvae spend nearly 9x longer handling size-matched bean aphids than pea aphids (Chapter 2) suggesting that convergent ladybird larvae may be limited by time rather than aphid abundance on the bean aphid diet.

Interestingly, ladybird larvae readily consumed bean aphids even if pea aphids were available in excess. Moreover, ladybird larvae consumed significantly more bean aphids than pea aphids on the mixed diet despite the negative effects of bean aphids on ladybird larval performance. This ostensibly suboptimal foraging behavior might be the result of effective antipredator behavior by pea aphids [14] that reduced the capture success of ladybird larvae even in the relatively simple environment of a plastic vial (i.e., by dropping from sides and lid). Indeed, pea aphids are less vulnerable than bean aphids to predation by convergent ladybird adults in laboratory tests on alfalfa plants [2]. Our results are consistent with the growing appreciation that predatory insects commonly select prey for factors (e.g., mobility) other than nutritional value [9, 42].

Our experiments were conducted in an artificial laboratory setting lacking foraging cues that are present in the field. Aphid honeydew is used as a foraging cue in some aphid-ladybird systems [5, 18], but convergent ladybird larvae do not discriminate between bean and pea aphids based on aphid honeydew [37]. It is also possible that ladybird larvae may avoid unsuitable aphids through the oviposition decisions of adult ladybird beetles. However, it is largely unknown whether ladybird beetles preferentially oviposit near suitable aphid species [15, 32]. Besides, fields, and even individual plants, are likely to contain more than one prey species, which complicates the oviposition decisions of generalist predatory insects. Thus, there is little evidence to suggest that ladybird larvae may use other mechanisms to avoid consumption of unsuitable aphids in the field, but this is a largely unexplored area.

The continued spread of bean aphids in North America poses a considerable foraging challenge for convergent ladybird beetles. In the absence of avoidance or tolerance mechanisms, the consumption of bean aphids could have dramatic fitness consequences for convergent ladybird larvae. Selection experiments in a laboratory setting have shown that ladybird beetles are capable of relatively rapid evolution for improved performance on previously unsuitable food [39], but the interactions of generalist predators with any one prey species in the field may be relatively weak, thereby limiting the potential for rapid evolution. The relationship between the relative abundance of bean aphids and the selective pressure for convergent ladybird larvae to avoid, or tolerate, consuming bean aphids presents an interesting case study in the evolutionary dynamics of a novel predator-prey association.

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Chapter 2

Beyond diet choice: predator behavior after consuming unsuitable prey

2.1 Abstract

Non-lethal effects of predators on prey behavior play a prominent role in structuring ecological communities, but the potential for prey to affect predator behavior has been largely overlooked. Prey can influence predator behavior through sublethal effects associated with chemical defenses. Because the compounds associated with chemical defenses in prey species are often not known, prey suitability is assessed by measuring the performance (e.g., growth, development, survival) of predators feeding on a prey species and toxicity is inferred indirectly from very low suitability. However, predator behavior may also provide indirect inference of the presence of toxins. As a case study, we measured the effects of consuming a single, unsuitable prey item on the behavior of ladybird beetle larvae. We documented significant effects of consuming unsuitable

prey in four behaviors: handling time, inactivity, intensive search, and patch-leaving tendency. Moreover, the strength of the effect of consuming unsuitable prey depended on the predators hunger level for half of the behaviors measured. Overall, consumption of unsuitable prey induced lethargic behavior by predators (i.e., longer handling times, longer bouts of inactivity, shorter bouts of intensive search, and lower patch-leaving tendency) relative to consuming suitable prey, suggesting the presence of toxins in the unsuitable prey. The sublethal effects of consuming unsuitable, possibly toxic, prey may reduce the foraging efficiency of the predator. We suggest that research on predators and toxic prey should extend beyond questions of behavioral avoidance and physiological tolerance to include the sublethal effects of consuming toxic prey on predator behavior.

2.2 Introduction

Predator-prey dynamics have important implications for ecosystem structure and function [52, 57] with classic examples (e.g., otter/urchin [46], wolf/moose [41], lynx/hare [33]) playing a critical role in shaping our understanding of ecological systems. Traditional examinations of predator-prey interactions have focused on lethal effects and the corresponding population and community responses, but it is becoming increasingly apparent that non-lethal effects are equally important [37, 49]. Still, most studies consider the influence of non-lethal effects only from the perspective of predation risk influencing prey behavior and often ignore the potential for prey to have effects on predator behavior [27]. One way for prey to affect predator behavior is to synthesize chemicals (toxins) that are sublethal for the predator if consumed in small amounts.

Predators cope with toxic prey through behavioral avoidance [34] and/or physiological detoxification [8]. However, predators also consume toxic prey for which they have no physiological tolerance [13]. Consumption of toxic prey may be particularly likely when non-toxic prey are scarce or toxic prey are novel. Scarcity of non-toxic prey leads to consumption of toxic prey because predators respond to the threat of starvation by including low-quality and toxic prey items in their diet [15, 59, 62]. Even when non-toxic prey are abundant, the availability of non-toxic prey to predators may be depressed because they are difficult to catch and subdue [35, 50]. Generally, the trade-off between chemical defense and alternative defense mechanisms [47] suggests that predators can capture toxic prey more easily than non-toxic prey. Indeed, the vulnerability of prey to predation often plays a more prominent role in predators' diet selection than the nutritional quality or toxicity of prey [60]. Novelty of toxic prey leads to consumption of toxic prey because, before learning to reject the toxic prey, predators typically sample at least one, and often several, toxic prey items [55]. Even predators that possess innate avoidance [9] or physiological tolerance [8] of toxic prey are vulnerable to novel chemical defenses in exotic prey [61]. For both developmental and evolutionary time scales, therefore, prey novelty may increase the likelihood of consuming toxic prey.

In this paper, we present a case study that demonstrates the potentially deleterious, but sublethal, effects of consuming an unsuitable, possibly toxic, prey species on predator foraging behavior. Through the case study, we illustrate the value of measuring predator behavior for inferring the existence of toxins in prey species and the potential importance of the sublethal effects of toxic prey on predator foraging efficiency. Specifically, we examined the effect of consuming a single unsuitable prey item on predator behaviors—handling time, activity, intensive search, patch-leaving tendency—that are likely to influence subsequent foraging success. We also manipulated hunger level of the predators because many foraging decisions are state-dependent [11, 64] and the magnitude of the post-consumptive effects of unsuitable prey may depend on the predator's state.

We used ladybird beetles and their aphid prey as a case study because ladybird-aphid systems possess attributes that may increase the likelihood of consuming of unsuitable prey. For example, ladybird beetles respond to scarcity of suitable prey in the field by expanding their diet to include low-quality food, such as toxic aphids, small insect larvae, insect eggs, mites, nectar, and honeydew [15, 62]. Even when suitable prey are abundant, ladybird beetles show limited ability to avoid unsuitable/toxic prey in laboratory studies [5, 19, 44, 45, see also Fig. 1.2]. Aphids have developed different anti-predator strategies that may make toxic species easier to capture than non-toxic species. For example, some species invest in chemical defense [48] whereas other species defend themselves by kicking, walking away, or dropping off the plants [14, 43]. Moreover, numerous non-native species of both ladybird beetles [28] and aphids [21] are found in North America, leading to potentially novel species assemblages.

2.3 Methods

2.3.1 Model system

The convergent ladybird beetle (*Hippodamia convergens*) is one of the most abundant native ladybird beetles in North America. Black bean aphids (*Aphis fabae*) and pea aphids (*Acythrosiphon pisum*) are unsuitable (Chapter 1) and suitable prey [24] for *H. convergens*, respectively, but it is unknown if bean aphids possess toxins. The assessment of prey suitability for ladybird beetles typically involves measuring predator performance in laboratory feeding trials rather than direct measurement of the energy content, nutrient composition, or toxic compounds of the prey. For the larval stage, prey species that support development to the adult stage are considered suitable prey with the degree of suitability dependent on the developmental rate and/or adult mass [42]. Toxicity may be inferred indirectly through very low larval survival, such as for convergent ladybird larvae feeding on bean aphids (Table 1.2). Bean and pea aphids differ in the ability to escape predation with bean aphids much less likely than pea aphids to respond to predator activity by dropping from plants [43], which is a highly effective behavior for reducing predation by ladybird beetles [23]. Both aphid species were introduced to North America over 130 years ago [21].

2.3.2 Insect rearing

We maintained separate cultures of each aphid species with broad beans (*Vicia faba*) as the host plant. Adult ladybird beetles were housed in cages with pea aphids and broad bean plants. To avoid egg cannibalism, we removed ladybird eggs from the culture and placed them in a separate cage for hatching. We placed recently hatched (< 24 hrs) ladybird larvae in individual plastic vials and fed them excess fresh pea aphids daily. By rearing ladybird larvae individually, we avoided cannibalism and knew the age of all larvae. All insects were maintained at approximately 24°C on a 16:8 hour photoperiod.

2.3.3 Experimental arena

We used experimental arenas comprised of a compound broad bean leaf (2 leaflets) adhered to an agar plate (150 x 20 mm Petri dish with 3 ml of 2% agar containing 1 g/L of Miracle-Gro). The arenas maintained some of the foraging cues associated with ladybird larvae searching for aphids on a plant, while allowing for the detailed video recording of ladybird movements. We estimated leaf area for each arena with image analysis software [1]; leaf area was similar in both the bean and pea aphid trials

(Welch two-sample t-test: $t = -1.18, df = 120, p = 0.24$; bean $= 48.8 \pm 1.0$ cm^2, pea $= 47.0 \pm 1.2$ cm^2). Ladybird larvae were moved to the experimental arena on either a fresh piece of broad bean stem ($\approx$ 3 cm long) or a camelhair brush.

2.3.4 Behavioral trials

Behavioral trials consisted of placing a ladybird larva on a leaf in an experimental arena and placing either a bean or pea aphid near the ladybird's mouthparts. We used an adult bean aphid or a similarly-sized pea aphid (matched by eye) because apterous pea aphid adults ($\approx$ 3.8 mg) are 4x larger than apterous bean aphid adults ($\approx$ 0.9 mg) [16]. Trials started when the ladybird larva secured the aphid in its mouthparts and ended when the ladybird larva was no longer touching any part of the leaf or stem in the experimental arena. At the end of the trial, we noted whether the aphid was partially or fully consumed. All trials were videotaped from directly above the experimental arena. Four behaviors were quantified from the video recordings (see Section 2.3.5).

Each ladybird larvae was used only once. We used 4th-instar ladybird larvae in the behavioral trials because it is the most voracious life stage. Within 1 or 2 days of reaching the 4th instar, we removed all aphids from the ladybird larva's vial to initiate a starvation period ranging from 2-24 hrs (see Fig. C.1 for distribution of starvation periods). We considered the pre-trial starvation period as a proxy for hunger level.

2.3.5 Overview of video analysis

We recorded video for 125 behavioral trials. Movement paths were digitized for 93 videos with automated tracking software (Viewer, BIOBSERVE) and 18 videos with manual tracking software (Tracker, Douglas Brown, Cabrillo College). Fourteen videos

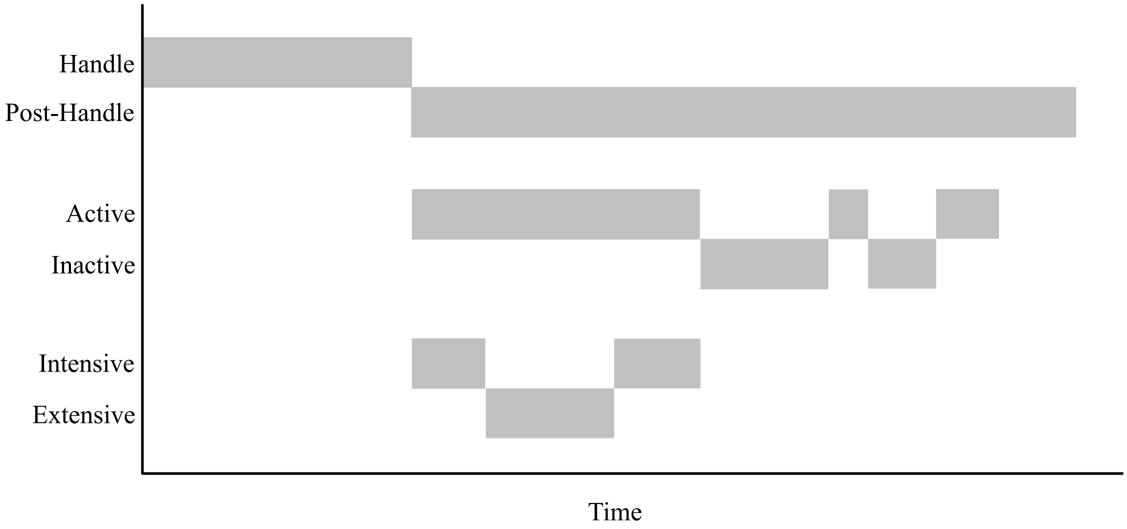

Figure 2.1: Example of how ladybird larvae behaviors were scored in the video analysis of a single behavioral trial. Movements from the first 90 min of post-handling time were digitized and divided into bouts of activity and inactivity. The first bout of activity was divided into bouts of intensive and extensive search.

were not digitized because of poor video quality. We digitized movement paths at 1-sec intervals from the end of aphid handling until the earlier of when the ladybird larva left the leaf or when 90 min had elapsed.

Handling time began when the predator secured the aphid in its mouthparts and ended when the predator moved away from the feeding site. Post-handling time spanned from the end of aphid handling until the predator was no longer touching any part of the leaf or stem in the experimental arena. Thus, post-handling time equaled patch residence time minus handling time. All 125 videos were scored for handling time and post-handling time.

Post-handling time ($\leq$ 90 min) was divided into bouts of activity and inactivity (Fig. 2.1; see Appendix A for details). The first bout of activity was then divided into bouts of intensive and extensive search (Fig. 2.1). Intensive search behavior is characterized by slow speeds and frequent turns whereas extensive search involves comparatively fast, direct movement. We classified movements as intensive or extensive with a general and robust method based on the time spent in the vicinity of path locations [3, see Appendix A for details]. The method, therefore, captures the essence of intensive search in a single measure (i.e., time spent in areas along the path) rather than two measures (i.e., speed and turn angle).

2.3.6 Statistical analysis

We used Cox proportional-hazards regression to analyze the effect of aphid type, starvation period, and the interaction between aphid type and starvation on the likelihood that predators stop a particular behavior at any point in time. The Cox model assumes that predators have a basic tendency to stop a certain behavior (baseline hazard), which is reset at renewal points. In our case, renewal points were the beginning of behavioral bouts (e.g., handling aphid, intensive search). The observed hazard rate is the product of the baseline hazard and a factor that gives the joint effect of a set of covariates. The form of the baseline hazard is left unspecified, but the covariates enter the model linearly [22]. The baseline hazard and the regression coefficients are estimated with likelihood maximization [12]. The Cox model allows for the inclusion of records where the end of the behavioral event was not observed (i.e., right-censoring). One and six percent of handling and post-handling bouts, respectively, were censored because the hard drive of the video camera reached capacity. Two percent of inactive bouts were censored because we only analyzed activity patterns for the first 90 min of post-handling time. Nineteen percent of intensive search bouts were censored because we only analyzed intensive search behavior for the first bout of activity.

Each trial included a single feeding event and ended when the predator left the leaf.

Thus, the Cox models for handling and post-handling time included a single behavioral bout for each individual (Fig. 2.1). However, the Cox models for inactive time and intensive search time included multiple behavioral bouts for each individual (Fig. 2.1), which likely violates the assumption that each behavioral bout was an independent event. However, parameter estimates [38] and jackknife variance estimates [39] in Cox models are robust to violation of the independence assumption. We looked at plots of the scaled Schoenfeld residuals for each model for evidence of violation of the proportional hazards assumption [22].

To visualize the results of our survival models, we characterized the survival function for each response variable by the average tendency to stop a behavior. The average tendency refers to the time when the model predicts that 50% of the predators would end a behavioral bout. We re-sampled the data with replacement (i.e., bootstrap method) 1000 times for each response variable; estimated a new survival model and predicted the time to 50% over the full range of starvation periods for each bootstrapped data set; and, calculated the mean and 95% quantiles of the distribution of times to 50% for each starvation level.

The results from the survival models are reported in terms of the duration of behavioral bouts, so it is important to emphasize the relationship between the bout duration and the regression coefficients (β-values). Negative regression coefficients indicate longer bouts of a behavior because the likelihood of the bout ending is reduced relative to the baseline hazard, and vice versa for positive regression coefficients. For all of our survival models, the baseline hazard was estimated for a ladybird larva that was starved for 2 hrs (smallest starvation period) and fed a pea aphid. A significant aphid effect, therefore, indicated that ladybird larvae starved for 2 hrs and fed a bean aphid were either more or less likely to end a behavioral bout than ladybird larvae starved for 2 hrs and fed a pea aphid. A significant starvation effect indicated that increasing the starvation period either increased or decreased the likelihood of ending a behavioral bout by ladybird larvae that were fed a pea aphid. A significant interaction term indicated that the effect of aphid type was not constant across all starvation levels. We retained the interaction term in the model only if it was at least marginally significant ($p < 0.10$).

Our primary focus was on the analysis of the duration of behavioral bouts. However, we conducted several additional tests to examine whether the type of aphid fed to a ladybird larva affected the probability and frequency of focal foraging behaviors. We used proportion tests to determine if aphid type affected 3 behaviors: (1) probability that an aphid was fully consumed, (2) probability that a ladybird larva engaged in any bouts of inactivity, and (3) probability that a ladybird larva engaged in any bouts of intensive search. We used generalized linear models to test if aphid type affected the number of bouts of inactivity (negative binomial error distribution) or intensive search (Poisson error distribution) for each ladybird larva. The negative binomial distribution was used to account for overdispersion in the inactivity data. We used R for all statistical analysis [51], including the survival package for Cox proportional-hazards regression and the MASS package for negative binomial GLM.

2.4 Results

2.4.1 Handling time

Ladybird larvae were significantly less likely to fully consume bean than pea aphids ($\chi^2 = 89.02, df = 1, p < 0.001$; bean: 15%, pea: 100%). Despite the prevalence of partial consumption of bean aphids, ladybird larvae spent significantly more time handling bean than pea aphids ($\beta = -2.192, se = 0.490, z = -4.475, p < 0.001$; Fig.

2.2A). In general, predators spend more time handling mechanically or chemically defended prey than undefended prey because of the extra pre- or post-consumption processing time required [31, 63]. As the starvation period increased, time spent handling pea aphids decreased ($\beta = 0.040, se = 0.021, z = 1.919, p = 0.055$; Fig. 2.2A). In contrast, handling time increases with increasing hunger in another species of ladybird larvae (*Coccinella septempunctata*) [10]. The difference between handling bean and pea aphids also increased as the starvation period increased (interaction term: $\beta = -0.064, se = 0.030, z = -2.131, p = 0.033$; Fig. 2.2A), which suggests that hungry ladybird larvae are more strongly affected by consuming bean aphids than satiated ladybird larvae.

2.4.2 Post-handling time

Post-handling time decreased as the starvation period increased for ladybird larvae fed pea aphids ($\beta = 0.065, se = 0.021, z = 3.106, p = 0.002$; Fig. 2.2B) because hungry ladybird larvae were more active (see Section 2.4.3), and, thus, more likely to leave the patch. As the starvation period increased, the difference in post-handling time between ladybird larvae fed bean and pea aphids increased (interaction term: $\beta = -0.059, se = 0.029, z = -2.025, p = 0.043$; Fig. 2.2B), but the effect of aphid type was effectively zero for satiated ladybird larvae ($\beta = 0.063, se = 0.408, z = 0.155, p = 0.877$; Fig. 2.2B), which again suggests that hungry ladybird larvae are more strongly affected by consuming bean aphids than satiated ladybird larvae. The increased time in the patch for hungry ladybird larvae fed bean aphids stemmed from longer bouts of inactivity (see Section 2.4.3).

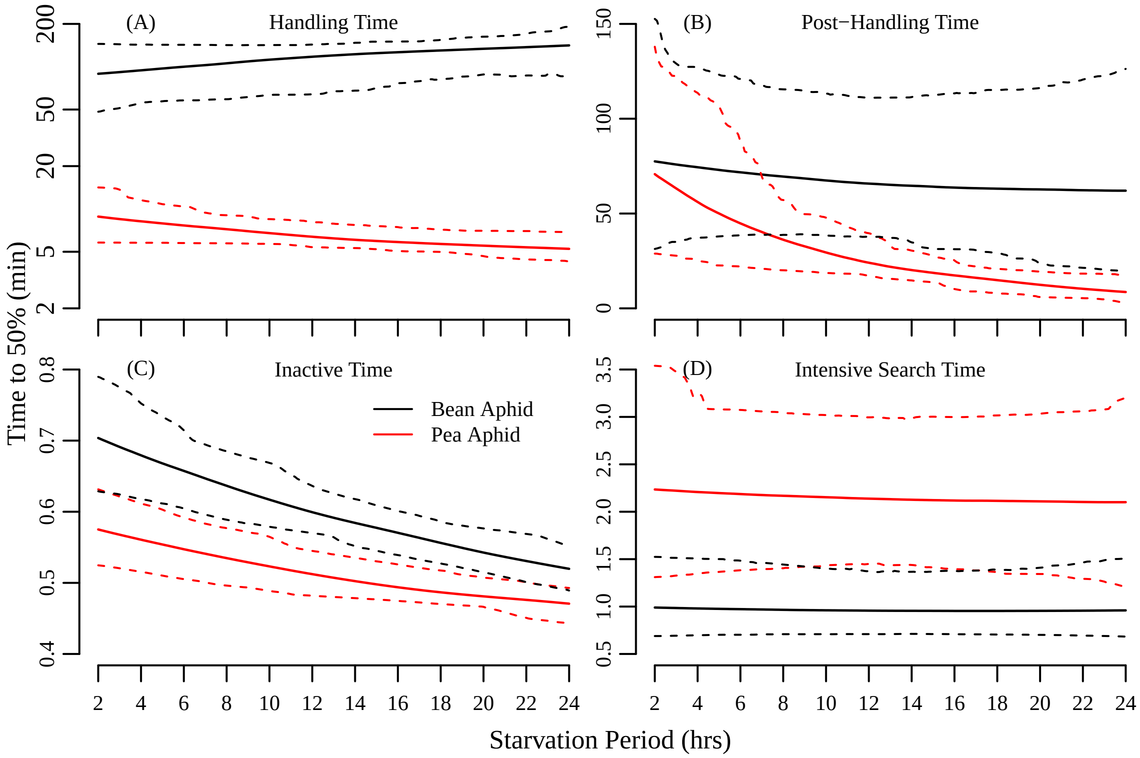

Figure 2.2: Visualization of results from Cox's proportional-hazards regression analysis of behavioral bouts exhibited by ladybird larvae fed either a bean or pea aphid. For each behavior, we display the time when 50% of predators are predicted to end a behavioral bout. Solid lines represent the mean time to 50% across 1,000 iterations of a bootstrap procedure and dashed lines represent the 95% quantiles of the distribution. Note the $\log_2$ scale for the y-axis in panel A.

2.4.3 Inactive time

Not all ladybird larvae engaged in bouts of inactivity ($N_{\text{pea}} = 27$ of $56, N_{\text{bean}} = 40$ of 55), but ladybird larvae fed bean aphids were more likely to show inactivity ($\chi^2 = 5.98, df = 1, p = 0.014$; bean: 73%, pea: 48%), engaged in more bouts of inactivity ($t = 3.31, df = 66, p < 0.001$; bean: 21.83 ± 3.55, pea: 9.22 ± 1.88), and exhibited longer bouts of inactivity ($\beta = -0.286, se = 0.092, z = -3.095, p = 0.002$; Fig. 2.2C) than ladybird larvae fed pea aphids. Reduced activity is a typical response to consumption of toxins from both natural (e.g., plants, prey) [30, 40, 56] and anthropogenic sources (e.g., herbicides, pesticides) [7, 30, 53]. The duration of bouts of inactivity decreased as starvation period increased ($\beta = 0.022, se = 0.007, z = 2.923, p = 0.003$; Fig. 2.2C). Generally, satiated predators are inactive predators [2, 29]. There was no significant interaction between aphid type and starvation period ($p > 0.10$). In contrast, salamanders increased activity with increasing hunger, but not when exposed to pesticides (i.e., significant hunger-by-toxin interaction) [53].

2.4.4 Intensive search time

Not all ladybird larvae moved far enough for us to divide the first bout of activity into bouts of intensive and extensive search ($N_{\text{pea}} = 42$ of 54, $N_{\text{bean}} = 28$ of 51), but ladybird larvae fed pea aphids were more likely than ladybird larvae fed bean aphids to have moved far enough for us to identify bouts of intensive search ($\chi^2 = 5.19, df = 1, p = 0.022$; bean: 55%, pea: 78%). Only 54% of ladybird larvae in our study engaged in intensive search immediately after eating an aphid, despite the conventional wisdom that predators should follow prey consumption with intensive search [4]. Similarly, predators should follow intensive search with extensive search, but ladybird larvae typically switched back and forth between intensive and extensive search exhibiting high inter-individual variability in the temporal sequence of search behavior [18]. Ladybird larvae fed bean aphids engaged in a similar number of intensive search bouts ($z = -0.816, p = 0.415$; bean: 1.29 ± 0.21, pea: 1.52 ± 0.19), but had shorter intensive search bouts ($\beta = 0.779, se = 0.259, z = 3.014, p = 0.003$; Fig. 2.2D) than ladybird larvae fed pea aphids. The duration of intensive search bouts was not affected by the starvation period ($\beta = 0.002, se = 0.018, z = 0.092, p = 0.927$; Fig 2.2D) and there was no significant interaction between aphid type and starvation period ($p > 0.10$). In contrast, intensive search time increases with increasing hunger in another species of ladybird larvae (*C. septempunctata*) [10].

Shorter bouts of intensive search for ladybird larvae fed bean aphids have 3 possible explanations: (1) prey novelty, (2) prey suitability, and (3) toxic interference. Bean aphids were novel prey because the diet prior to the behavioral trials consisted entirely of pea aphids. Thus, our findings may simply indicate that encounters with novel prey involve less intensive search than encounters with familiar prey [17]. Reduced intensive search after consuming bean aphids could also reflect an adaptive response to prey suitability [32, 36] because shorter bouts of intensive search should lead to less time spent in patches with unsuitable prey. However, we suggest that consuming toxic prey interferes with the ability of the predator to adjust its intensive search behavior to the properties of the prey or patch. Our interpretation of reduced intensive search as a sublethal effect of consuming toxic prey is also consistent with the general lethargy observed in all behaviors measured in this study. Future work should address the abilities of ladybird larvae, which are slow learners [6], to adaptively adjust intensive search behavior to prey suitability.

2.5 Discussion

We documented dramatic effects of consuming a single bean aphid on the behavior of ladybird larvae. In general, ladybird larvae that ate bean aphids exhibited lethargic behavior (i.e., longer handling times, lower patch leaving tendency, longer bouts of inactivity, and shorter bouts of intensive search) that might indicate the presence of toxins in bean aphids, particularly considering the low larval survival of convergent ladybird larvae on a bean aphid diet (see Table 1.2). The lethargy associated with eating a single bean aphid could reduce the consumption rate over longer time periods. Although subsequent encounters with non-toxic prey may diminish the sublethal effects of consuming toxic prey, actively hunting predators, like ladybird beetles, are unlikely to encounter additional prey while in such a lethargic state. The abundance of non-toxic prey, therefore, should not influence the duration of the toxic effect after consumption of a toxic prey item. However, the abundance of non-toxic prey should influence the magnitude of the toxic effect, which was greatest for hungry predators. Interestingly, one of the conditions that makes the consumption of toxic prey likely (i.e., scarcity of non-toxic prey) also makes the impact of the sublethal effect of toxic prey the greatest.

Inactive predators acquire fewer resources and grow more slowly than active predators [66]. In the short term, the effect of toxic prey, therefore, may be to reduce prey consumption through lower foraging efficiency. Consumption of toxic prey may also reduce prey consumption over longer time scales because consuming toxic prey can stunt predator growth [20, 61] and prey consumption rate increases as predators grow [26, 65]. Slower predator growth rates could also increase susceptibility to their own predators if they escape predation by growing to a larger size [58, 65]. However, reduced predator activity is not without benefits. For example, inactive individuals are generally regarded as less susceptible to predation because movement often increases detection and inactive individuals are often hiding in refuges [66]. Consumption of toxic prey, though, leads to predator immobilization at a feeding site, exposed to predation, rather than in a refuge. Thus, toxic prey may alter the classic growth/mortality tradeoff by reducing foraging efficiency and increasing predation risk. Given the numerous potential effects of consuming toxic prey, which often comprise a considerable proportion of the available arthropod prey in a habitat [25, 54], we suggest that research on predators and toxic prey should extend beyond questions of behavioral avoidance and physiological tolerance to include the sublethal effects on predator behavior after consuming toxic prey.

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Chapter 3

Foragers should use sensory cues, not resource encounters, to determine when to switch between intensive and extensive search modes

3.1 Abstract

Abiotic and biotic processes lead to spatial heterogeneity in the distribution of resources. Foragers can exploit aggregated resources with composite search behavior comprised of intensive and extensive search modes. Most composite search models assume that animals switch search modes based on resource encounters, but animals also use sensory cues (e.g., olfaction, vibration) to modify search behavior. We developed a modeling framework to compare the performance of composite search strategies based

on either resource encounters or sensory cues. We compared the search strategies across different degrees of resource aggregation and examined the performance of the search strategies in response to changes in resource aggregation to test the robustness of the search strategies to environmental change. We found that the search strategy based on sensory cues outperformed the search strategy based on resource encounters across the full spectrum of resource aggregation and was more robust to changes in resource aggregation. Our results suggest that natural selection should favor foragers that switch modes based on sensory cues over those that use resource encounters.

3.2 Introduction

Features of the physical environment (e.g., soil texture and moisture) and biotic processes (e.g., competition, dispersal) lead to spatial heterogeneity in the distribution of food resources [13, 24, 32]. The degree of resource aggregation varies over time [6, 33] and depends on both the type of resource [2, 47] and the spatial scale of observation [11]. Foragers can exploit aggregated resources by focusing search effort on areas rich in resources and quickly traversing sparser regions. This search tactic is known variously as composite search [31], area-restricted search [45], area-concentrated search [7], or intermittent search [9]. Composite search behavior is widespread, observed in taxa as diverse as slime moulds [25], insects [14], fish [20], birds [28], and mammals [17]. A forager using a composite search strategy alternates between intensive and extensive search modes. In intensive mode, a forager thoroughly searches resource rich areas by making short moves and reorienting frequently whereas, in extensive mode, it moves directly across resource poor areas by making long, straight-line moves with few interruptions.

The empirical evidence for composite search behavior is extensive, but the proximate mechanisms that trigger transitions between intensive and extensive search are poorly understood. When resources are aggregated, animals can use resource encounters as a proximate cue of the local resource density [10, 15]. Thus, foragers can exploit resource aggregations by searching intensively after resource encounters. As resources become depleted, resource encounters become infrequent, and foragers should switch to extensive search to relocate to a more profitable foraging area. However, resource encounters do not always trigger intensive search behavior [14, 45, Chapter 2]. Instead, foragers may use olfactory [27] or tactile [23] cues to trigger intensive search even in the absence of a resource encounter.

Models of composite search behavior have largely ignored the potential for animals to use sensory cues (e.g., olfaction, vibration) to modify search behavior [but see 18]. Rather, composite search models typically assume that animals only detect resources at close range and only use resource encounters as a cue for switching between extensive and intensive search behavior [7, 31, 38]. Models of composite search behavior, therefore, draw from a large body of work on the 'random search problem' [foraging context reviewed in 44], which addresses how to efficiently find targets with limited information about the location of the targets.

The ignorant foragers of random search models and the omniscient foragers of classic optimal foraging models [40] occupy opposite ends of a continuum of the amount of information available to foragers. However, foraging theory is increasingly incorporating constraints on the information available to foragers [3, 30] to produce a better fit between theory and data [42, 43]. Similarly, random search modeling might move profitably toward the center of the information continuum by extending the elegant mathematical tools of stochastic search strategies to include key foraging mechanisms, such as the use of sensory cues [e.g., 18, 37].

In this study, we developed a modeling framework to simulate composite search strategies with search mode transitions triggered by either resource encounters or sensory cues. Because resource encounters provide a more stochastic estimate of resource density than sensory cues, we compared the search strategies across different degrees of resource aggregation. We also examined the performance of the search strategies in response to changes in resource aggregation to test the robustness of the search strategies to environmental change. We found that the search strategy based on sensory cues outperformed the search strategy based on resource encounters across the full spectrum of resource aggregation and was more robust to changes in resource aggregation.

3.3 Modeling Framework

We built a simulation model in Netlogo [46] based on the following modeling framework. Resources were represented as points distributed across a landscape with different degrees of resource aggregation (see Appendix B for details). The forager had a fixed detection radius (Table 3.1), within which it could immediately detect resources. If no resources fell within this radius, the forager moved across the landscape according to a set of probabilistic movement rules. The stochastic nature of the forager's trajectory is a desirable model feature because it agrees with the movement patterns observed in many foraging animals, and because few animals possess the capability to execute a purely systematic search [41].

Foragers in our model used composite search strategies with either a giving-up time (GUT) or giving-up density (GUD) criterion for switching between intensive and extensive search modes. With the GUT switching rule, foragers switched to extensive search after a specified time had elapsed since the last resource encounter. With the GUD rule, foragers switched to extensive search when the local resource density

Table 3.1: Parameter values used in the simulation model.

Parameter	Value
Resources	
Initial number of resources	100, 400, 700, 1000
Number of clusters[1]	15
Radius of resource cluster[2]	4, 8, 16, 32, 64
Forager	
Speed (distance/time step)	0.25
Detection radius	0.5
Lévy exponent (μ)	
Extensive search mode	1.0, 1.2, 1.4, 1.6, …, 3.0
Intensive search mode	1.0, 1.2, 1.4, 1.6, …, 3.0
Mode-switching criteria[3]	
Giving-up time	0, 50, 100, 150, 200, …, 500
Giving-up density	0, 0.0005, 0.001, 0.002, …, 0.128, 0.256

[1] Poisson random variable with $\bar{x} = 15$
[2] Resource aggregation decreases with increasing cluster radius
[3] Forager employs only one mode-switching criteria in a run of the simulation

dropped below a specified level. In our model, GUD foragers evaluated density via a resource density field that was created by summing the contributions of multinormal distributions centered on each resource. The resulting field had a number of desirable features: the contribution of a given resource decayed with distance, the field varied continuously with location, and the field was maximal at places near dense clusters of resources and minimal at places far from resources. The resource density field could apply to any type of cue where the probability of detecting the cue decays with distance. For example, if each resource on the landscape emits a chemical signal, then diffusion would lead to a chemical concentration profile similar to the resource density field.

Traditional composite search strategies involve ballistic motion in extensive mode and Brownian motion in intensive mode [31]. In ballistic motion, the forager travels in a straight line until it encounters a resource. In Brownian motion, the forager traces a highly convoluted trajectory, frequently revisiting areas it has previously explored. Ballistic motion and Brownian motion occupy two ends of a rich spectrum of behavior. Lévy walks encompass movements that span the full spectrum of movement behavior. A forager moving via a Lévy walk chooses a move length from a power-law probability distribution. The power law is characterized by a parameter, μ, which can range between 1 and 3; the lower the parameter, the fatter the tail of the move length distribution. Lévy walks converge to ballistic motion at $\mu = 1$ and Brownian motion at $\mu = 3$. Lévy walks have previously been used in the extensive mode of composite search strategies [35]. In this paper, we allow for Lévy walk behavior in both the extensive and intensive search modes. In addition to capturing a wide spectrum of movement behavior, Lévy walks are scale-free, which means that the statistical properties of movement are not dependent on a particular scale [36], and are superdiffusive, which means the move length distributions have fat tails, a common characteristic of empirical data on animal movement [44]. The simplicity and scale-free elegance of Lévy walks make them the preferred modeling option for non-composite searches [36, 44], but the potential of Lévy walks as components of composite search strategies is largely unexplored [but see 35]. We also collected simulation data from a non-composite search strategy based on a Lévy walk to compare to the results for the two composite search strategies.

3.4 Model Analysis

3.4.1 Optimal parameters

We used a grid-based search of the parameter space in our simulation model to find the optimal parameter combination for each search strategy in each landscape type (see Appendix B for details). A search strategy is specified by three parameters, the μ values for the intensive (μ_{int}) and extensive (μ_{ext}) search mode, and the switching parameter (GUD or GUT). As shorthand, we refer to a forager using a particular combination of search parameters as a forager's phenotype. The phenotype that maximized searching efficiency in a landscape type was defined as optimal. We calculated searching efficiency as the number of resources consumed divided by the total distance moved, a rate-maximizing metric of efficiency commonly used in random search models [4, 5, 8, 26, 29, 31, 35]. We conducted numerous runs for every parameter combination because our simulation model contained stochasticity in forager movements and initial resource locations.

3.4.2 Sensitivity

We examined the sensitivity of searching efficiency to each search parameter by varying one search parameter while holding the other two parameters at their optimal values. We normalized the parameter values to fall between 0 and 1 to facilitate comparisons across the different ranges of the parameters, i.e., $\mu_{\text{ext}} = \mu_{\text{int}} = [1, 3], \text{GUT} = [0, 500]$, and $\text{GUD} = [0, 0.256]$. We calculated the proportional difference in searching efficiency as $D_{\text{S}} = (y - \bar{y}_{\text{O}})/\bar{y}_{\text{O}}$ where y was the searching efficiency for a single run and $\bar{y}_{\text{O}}$ was the mean searching efficiency for the optimal phenotype. We fitted smoothing splines to the relationship between D_{S} and the normalized value of each parameter for each landscape type. The shape of the smoothing splines provided an indication of the sensitivity of searching efficiency to changes in each parameter. In two cases (see Table 3.2), the optimal μ_{ext} and μ_{int} were the same, which made the best giving-up time parameter arbitrary. Thus, those landscape types were excluded from the sensitivity analysis.

3.4.3 Robustness

To assess the robustness of the optimal strategies to changes in resource aggregation, we examined how a search strategy that maximized the searching efficiency for one landscape type performed in landscape types with different degrees of resource aggregation. Specifically, we calculated robustness as $D_{\text{R}} = (\bar{y}_{i,j} - \bar{y}_{\text{o}})/\bar{y}_{\text{o}}$, where $\bar{y}_{i,j}$ was the mean searching efficiency in landscapes with cluster radius i for a forager that evolved in landscapes with cluster radius j and $\bar{y}_{\text{o}}$ was the mean searching efficiency for a forager that evolved in landscapes with cluster radius i (e.g., $\bar{y}_{4,4} = \bar{y}_{\text{o}}$). Robustness was only calculated for foragers that evolved in landscapes with either clumped ($j = 4$) or dispersed ($j = 64$) resources. We performed 500 runs for each parameter combination. Then we re-sampled the data with replacement (i.e., bootstrap method) 500 times for each landscape types and calculated the mean and 95% quantiles of the distribution of robustness values.

The sensitivity and robustness analyses were conducted with R [34].

3.5 Results

3.5.1 Optimal parameters

Our simulations identified optimal movement characteristics for intensive and extensive search modes. Interestingly, the optimal movement behavior in each mode depended on the mode-switching criterion (GUT vs. GUD). Most notably, the best GUT strategies involved ballistic motion in extensive mode ($\mu_{\text{ext}} = 1$) for all degrees of resource aggregation and the best GUD strategies involved Brownian motion in intensive mode ($\mu_{\text{int}} = 3$) for almost all degrees of resource aggregation (Table 3.2). Ballistic motion is the expected behavior in extensive mode because it maximizes the amount of the landscape searched by a forager [44]. Brownian motion is the expected behavior in intensive mode when resources are clumped because it allows a forager to thoroughly search areas with high densities of resources. GUD foragers profitably used Brownian motion even when resources were not aggregated whereas GUT foragers used less thorough search (lower μ_{int}) as resources became less aggregated (Table 3.2).

The conventional composite search strategy, which is comprised of ballistic and Brownian motion in the extensive and intensive modes, respectively, was only optimal in 17 of the 40 (42.5%) landscape types that we explored (Table 3.2). For the GUT rule, traditional ballistic/Brownian composite search was only optimal in landscapes with the most aggregated resources. However, the optimal GUD strategy approximated the traditional ballistic/Brownian search strategy, where $\mu_{\text{ext}} \approx 1$ and $\mu_{\text{int}} \approx 3$, in all landscape types. Thus, GUD foragers display starkly contrasting movement behaviors in intensive and extensive mode whereas the contrast in movement behaviors is landscape dependent for GUT foragers. On all but the most clumped landscapes, GUT foragers should not use Brownian motion in intensive mode, a result that differs from the assumptions of previous models of composite search [22].

Table 3.2: Parameter combinations for three different search strategies producing the highest mean searching efficiency for different resource densities and cluster radii. Resource aggregation decreases with increasing cluster radius.

Resource Density	Cluster Radius	NCS[1]	GUT Strategy			GUD Strategy		
		μ	μ_{ext}	μ_{int}	GUT	μ_{ext}	μ_{int}	GUD
100	4	1.6	1.0	3.0	250	1.2	3.0	0.0005
100	8	1.4	1.0	3.0	400	1.4	3.0	0.0005
100	16	1.2	1.0	2.6	250	1.6	3.0	0.0005
100	32	1.4	1.0	1.8	150	1.4	3.0	0.0005
100	64	1.2	1.0	1.4	100	1.6	3.0	0.0005
400	4	1.6	1.0	3.0	150	1.2	3.0	0.0005
400	8	1.6	1.0	3.0	150	1.2	3.0	0.0020
400	16	1.4	1.0	2.6	150	1.0	3.0	0.0010
400	32	1.2	1.0	2.0	100	1.0	3.0	0.0010
400	64	1.2	1.0	1.6	50	1.2	3.0	0.0040
700	4	1.6	1.0	3.0	100	1.2	3.0	0.0020
700	8	1.4	1.0	3.0	100	1.0	3.0	0.0010
700	16	1.4	1.0	2.6	50	1.2	3.0	0.0160
700	32	1.2	1.0	2.0	50	1.0	3.0	0.0320
700	64	1.0	1.0	1.0	—	1.0	3.0	0.0320
1000	4	1.8	1.0	3.0	100	1.0	3.0	0.0005
1000	8	1.6	1.0	3.0	100	1.0	3.0	0.0005
1000	16	1.4	1.0	2.4	50	1.0	3.0	0.0320
1000	32	1.4	1.0	2.0	50	1.0	3.0	0.0640
1000	64	1.0	1.0	1.0	—	1.0	2.8	0.0640

[1] Non-composite search strategy

3.5.2 Sensitivity

Searching efficiency was most sensitive to movement behavior in extensive mode, μ_{ext} (Fig. 3.1). Small deviations from the optimal μ_{ext}, where the proportional difference in searching efficiency is zero, produced small effects, but large deviations reduced searching efficiency by up to 70% (see Appendix C, Figs. C.2-C.5). In contrast, large deviations from the optimal movement behavior in intensive mode, μ_{int}, reduced searching efficiency by no more than 45% (Figs. C.2-C.5). The patterns in sensitivity of μ_{ext} and μ_{int} were qualitatively similar between the GUT and GUD strategies (Figs. C.2-C.5).

Searching efficiency was more sensitive to values below the optimal switching threshold parameter (GUT or GUD) than above (Figs. C.2-C.5). Setting the switching threshold to zero leads the forager to spend all of its time in one search mode (non-composite search strategy), which is more costly for the GUD strategy than the GUT strategy. For instance, setting the GUT parameter to zero, while holding μ_{ext} and μ_{int} at their optimal values, produced a non-composite search based on ballistic motion (Table 3.2), which reduced searching efficiency by $< 40\%$. In contrast, setting the GUD parameter to zero, while holding μ_{ext} and μ_{int} at their optimal values, produced a non-composite search strategy based on Brownian motion (Table 3.2), which reduced searching efficiency by $> 60\%$.

Traditional ballistic/Brownian search, where $\mu_{\text{ext}} = 1$ and $\mu_{\text{int}} = 3$, was not optimal for all landscape types (Table 3.2), but the fitness costs of using this strategy instead of the optimal search strategy were relatively small ($< 5\%$) for both GUT and GUD rules in all landscape types (Figs. C.2-C.5). Note, however, that one run of our simulation model represents a relatively short period in a foragers lifetime with the total number of periods depending on the lifespan of the species. Thus, even a 5% difference between

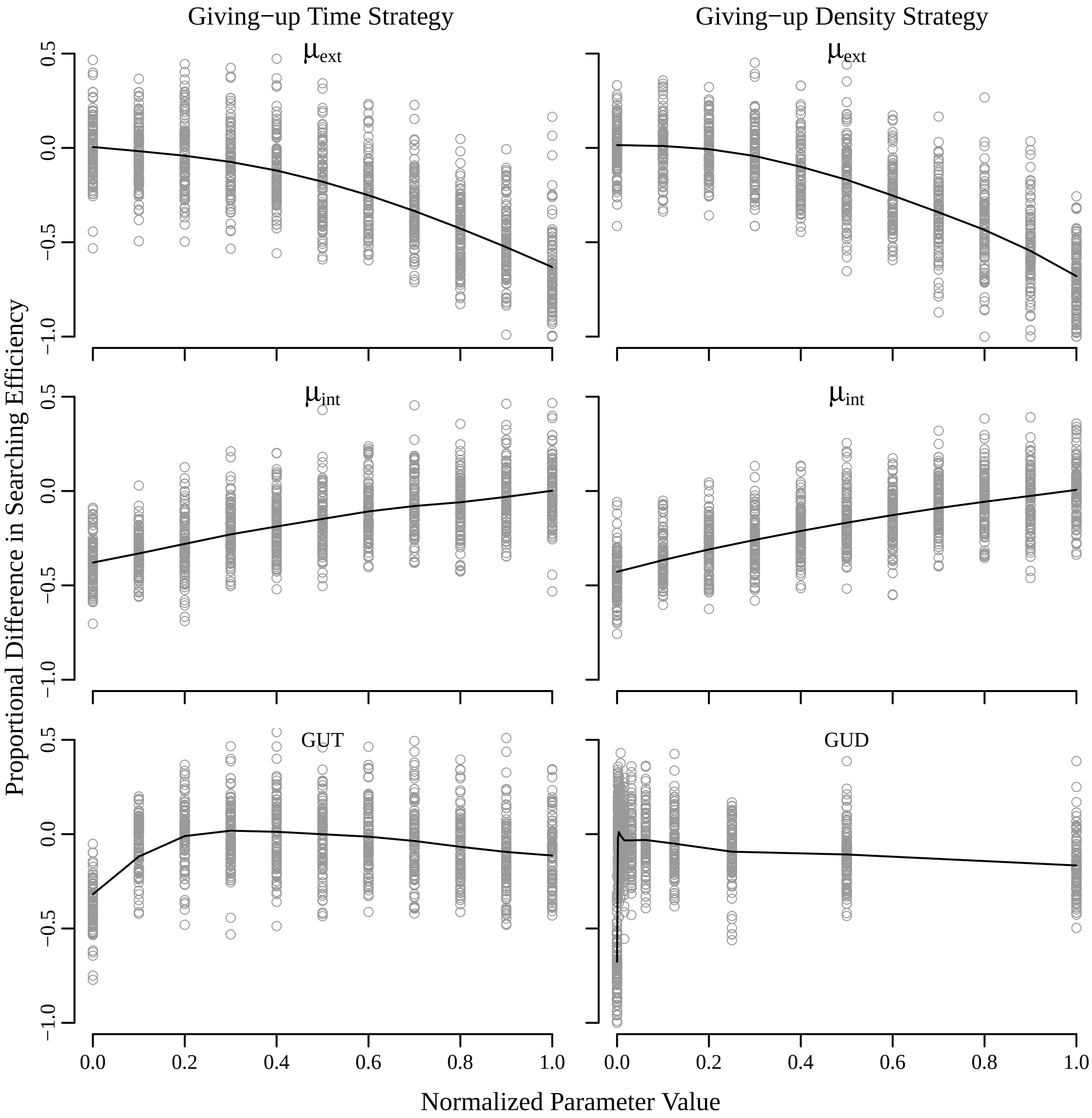

Figure 3.1: Representative example of sensitivity analysis for the three parameters associated with giving-up time and giving-up density strategies (resource density = 400; cluster radius = 4). Points represent proportional difference in searching efficiency for a single run relative to the mean searching efficiency produced by the optimal parameter combination. Parameter values were normalized for comparison. Lines represent smoothing splines fitted to the relationship. Sensitivity analysis based on 100 runs of the model for each parameter value. See text for additional details.

traditional ballistic/Brownian search and the optimal search strategy could provide a substantial advantage when compounded over the lifetime of a forager.

3.5.3 Robustness

The GUD strategy was less affected by changes in resource aggregation than the GUT strategy, particularly for foragers that were adapted to foraging for dispersed resources (red lines in Fig. 3.2). The optimal GUT strategy for harvesting dispersed resources approximated non-composite search behavior, i.e., similar values for the μ_{ext} and μ_{int} parameters (Table 3.2). Placing these foragers in landscapes with more aggregated resources drastically reduced their searching efficiency (red dashed lines in Fig. 3.2). In contrast, GUT foragers adapted to foraging for clumped resources were relatively robust to decreasing degrees of resource aggregation (black dashed lines in Fig. 3.2). The GUD strategy was relatively robust to deviations from the resource distribution pattern to which a forager was adapted (solid lines in Fig. 3.2).

3.5.4 Search strategy comparisons

The composite search strategies (i.e., GUT and GUD rules) outperformed the non-composite search strategy when resources were highly aggregated, but the relative advantage of composite search decreased as resource aggregation decreased (Fig. 3.3). Composite search also produced lower variability in searching efficiency than non-composite search when resources were highly aggregated (Fig. C.6). For all search strategies, both searching efficiency (Fig. 3.3) and variability in searching efficiency (Fig. C.7) decreased as resource aggregation decreased.

The GUD strategy performed better than the GUT strategy across the full spectrum of resource aggregation (Fig. 3.3). Previous work in a patch-use context has similarly

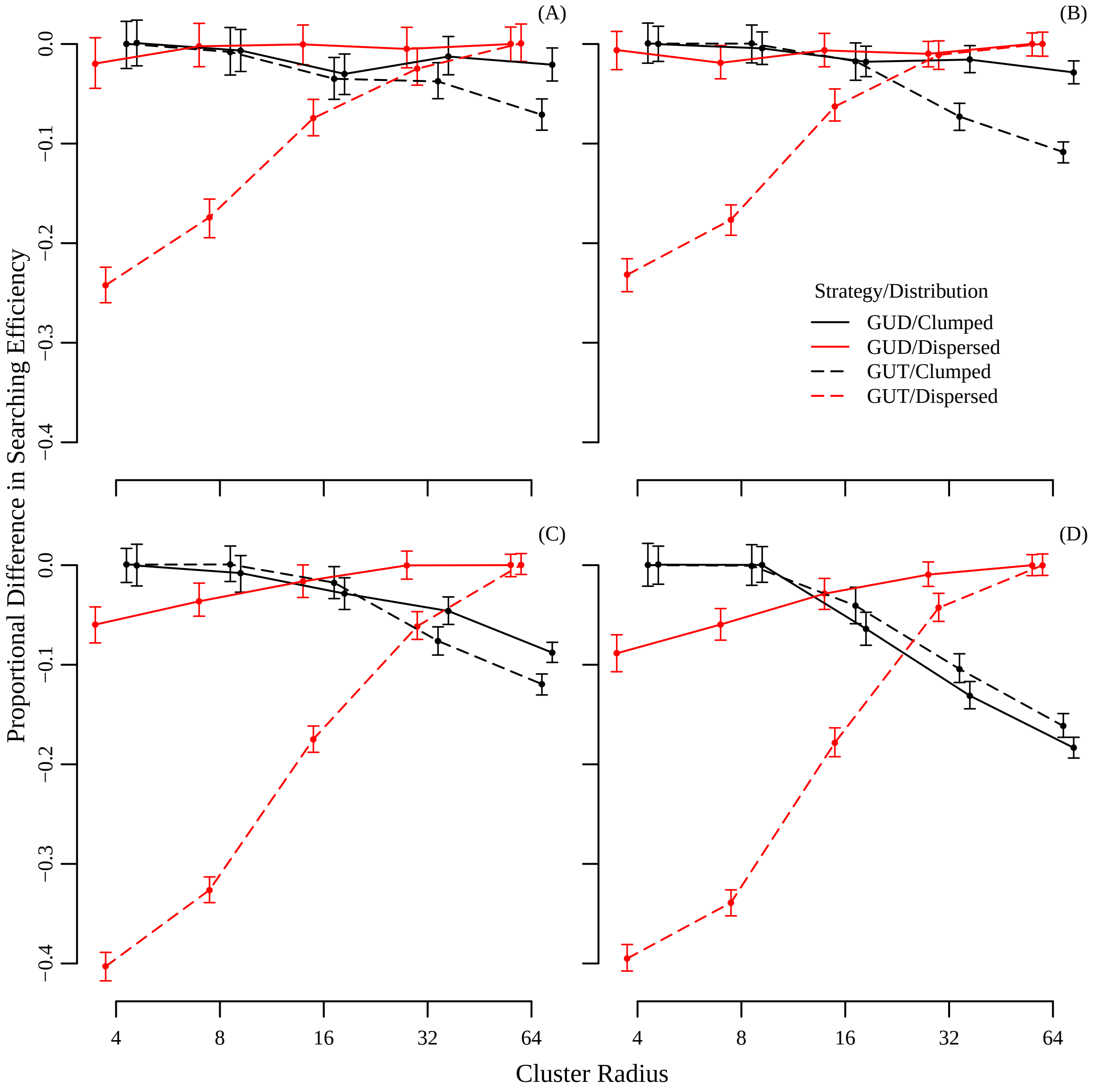

Figure 3.2: Robustness of composite search strategies across 5 levels of resource aggregation and 4 levels of resource density: (A) 100, (B) 400, (C) 700, (D) 1000. The performance of foragers that evolved in landscapes with clumped (black lines) or dispersed (red lines) resources was tested in landscapes with different degrees of resource aggregation. Robustness was calculated as the proportional difference in mean searching efficiency between a forager that is new to a landscape type and a forager that evolved in that landscape type. Points represent the mean proportional difference in searching efficiency, D_{R}, and error bars represent the 95% quantiles of the bootstrapped data set. See text for additional details. Points are offset from x-coordinates for clarity of presentation. Resource aggregation decreases with increasing cluster radius. The x-axis is presented on the $\log_2$ scale.

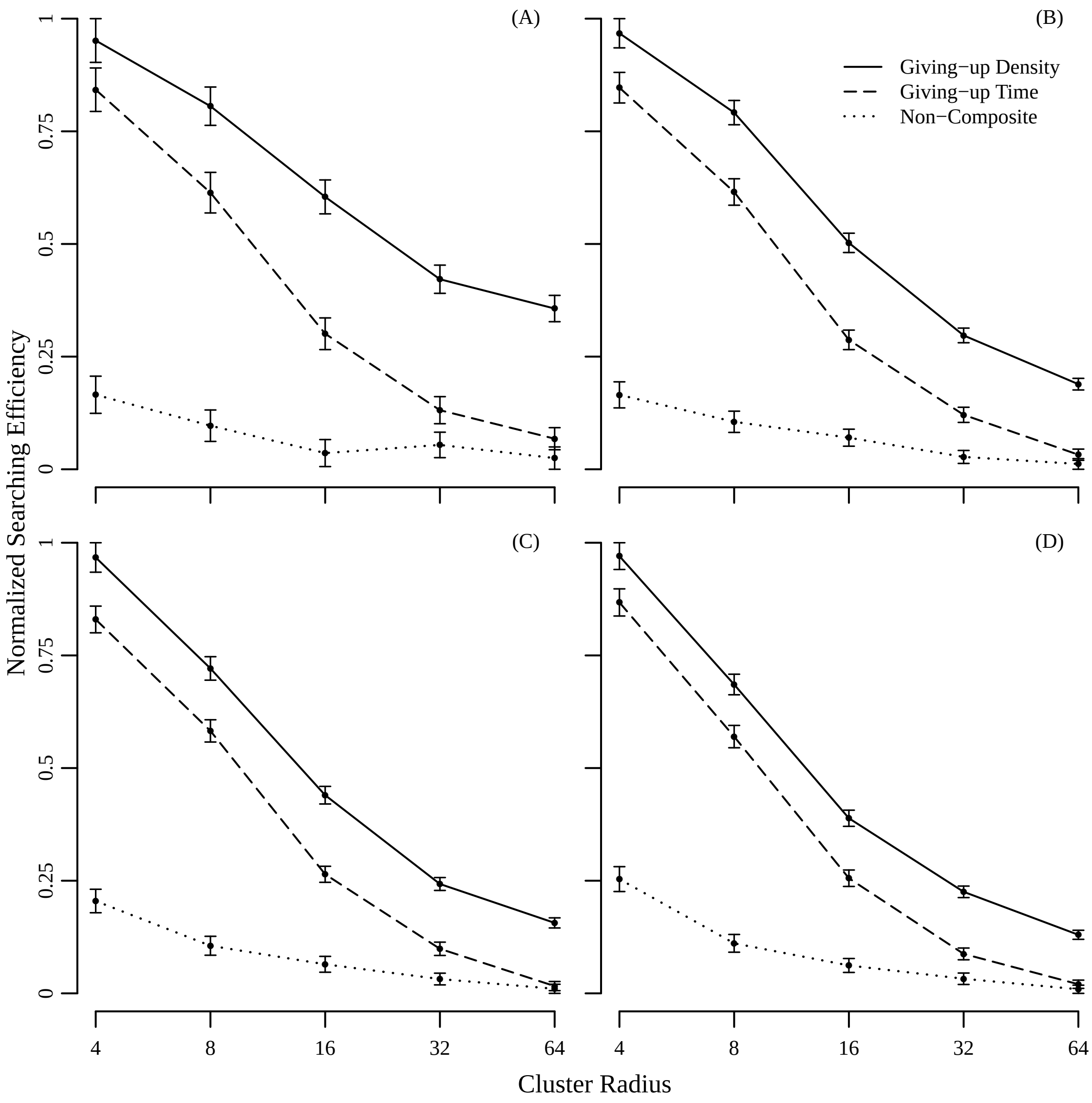

Figure 3.3: Normalized searching efficiency for three search strategies across 5 levels of resource aggregation and 4 levels of resource density: (A) 100, (B) 400, (C) 700, (D) 1000. Searching efficiency was normalized for comparison across resource densities. Resource aggregation decreases with increasing cluster radius. Error bars represent 95% confidence intervals. The x-axis is presented on the $\log_2$ scale.

shown that the GUT rule was outperformed by a patch-departure rule based on assessing patch quality [16]. Our work extends this previous result to show that the GUT rule is suboptimal for both clumped and dispersed resource distributions. The difference in performance between GUD and GUT foragers stems from more accurate and more frequent assessment of resource density by GUD foragers than GUT foragers. The GUD strategy is more accurate than the GUT strategy because the density estimate does not depend on the distribution of resources (see next paragraph). The GUD strategy allows for more frequent assessment because assessment occurs even in the absence of resource encounters. Because GUD foragers assess resource density at resource encounters and at the end of move lengths, GUD foragers make a relatively small commitment to intensive search when move lengths are short (i.e., $\mu_{\text{int}} \approx 3$). Moreover, GUD foragers are not obligated to switch to intensive search after resource encounters, as with the GUT strategy, which keeps GUD foragers from wasting time by searching intensively in areas with very low resource densities.

The advantage of the GUD strategy over the GUT strategy increased with decreasing resource aggregation (Fig. C.7). This can be explained by considering how the degree of resource aggregation impacts the ability of GUT and GUD foragers to determine when to engage in intensive search. On landscapes where resources are highly aggregated, a resource encounter indicates that other resources are nearby, and hence that it is worth searching intensively. Thus, the GUT strategy of switching to intensive search mode after a resource encounter is useful. On landscapes where resources are dispersed, a resource encounter does not necessarily indicate that other resources are nearby, and the GUT strategy provides no advantage over non-composite search (Fig. 3.3). In contrast, the GUD forager is able to use the resource density field to make assessments of which areas are profitable to engage in intensive search, even in the absence of resource aggregation. Although the resource density field for dispersed landscapes will be relatively homogenous, a GUD forager can still detect small peaks in resource density, which trigger intensive search.

3.6 Discussion

Spatial heterogeneity in the distribution of resources presents an important challenge for foraging animals. Composite search behavior allows animals to efficiently harvest aggregated resources, even when the resources do not occur in patches with perceptible boundaries [7]. Our central objective in this study was to use a simulation model to explore how the degree of resource aggregation affects the performance of composite search strategies based on either resource encounters (GUT rule) or sensory cues (GUD rule). To our knowledge, GUT is the only mechanism previously used in composite search models to approximate the optimal decision of when to switch between intensive and extensive search modes [e.g., 22, 31, 35] and, thus, our work is the first to include a GUD rule in a composite search model.

Our simulation results suggest that a GUD strategy confers a selective advantage over a GUT strategy. Our modeling framework, however, does not consider the costs involved in the evolution or development of sensory cues versus mechanisms for keeping track of time. More empirical work is needed on the the proximate cues that trigger intensive search, the costs and benefits of the proximate cues, and the prevalence of the different types of proximate cues in natural populations.

Composite search behavior has strong parallels with patch-use behavior. Intensive and extensive search equate to within- and between-patch search, respectively, and both GUT and GUD rules might allow foragers to approximate the optimal decision for switching search modes or leaving a patch. Composite search models can be applied to situations where resources do not occur in discrete patches with perceptible boundaries

[1, 7] and patch-use models are not directly applicable. However, composite search models have not yet been extended to consider ecological contexts (e.g., competition, predation risk) other than one forager searching for one type of resource and, thus, considerably lag the development of patch-use theory [12, 19, 21, 39]. It is important to evaluate when explicit consideration of the spatial distribution of resources alters the behavior of foragers and outcome of species interactions to justify the added complexity of spatially explicit models. The spatially explicit approach of random search models makes them appealing tools for making predictions about foraging behavior. Our results show, however, that the assumption of existing random search models that animals use GUT strategies should be revisited. Natural selection should favor animals that use sensory cues over those that rely on resource encounters to determine when to switch search modes.

3.7 Acknowledgements

Ben Nolting contributed extensively to model development, model analysis, and writing of this chapter. The supercomputing resources provided by the Holland Computing Center at the University of Nebraska-Lincoln greatly facilitated the collection of the simulation data reported in this study. Brigitte Tenhumberg, Robert Gibson, and Chad Brassil provided helpful comments on an earlier version of this chapter.

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Appendix A

Detailed Description of Video Analysis

Movements from the first 90-min of post-handling time were digitized at 1-sec intervals. To identify bouts of inactivity, we used the distance moved at each 1-sec interval to classify the ladybird larva as either moving (distance moved > 0) or not moving (distance moved $= 0$) in each 1-sec interval. However, ladybird larvae were tracked at the center of their body, so subtle movement at the end of their body was likely to have gone undetected. Similarly, imperfect identification of the ladybird larva's body outline relative to the background occasionally produced small changes in (x,y)-coordinates even though the ladybird larva did not move. To minimize the effect of small tracking errors, we identified a threshold for the minimum duration for a bout of inactivity, i.e., number of consecutive time steps where distance moved was zero. Choosing the threshold involved a tradeoff between classifying subtle movement as a bout of inactivity (low threshold) and classifying inactivity as subtle movement (high threshold). We counted the number of occurrences for each duration of inactivity within and across all movement paths and used kernel density estimates, which are non-

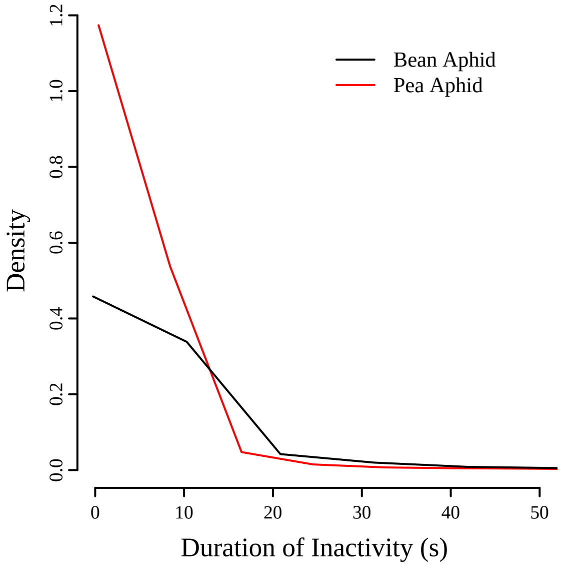

Figure A.1: Kernel density estimates for the duration of inactivity for ladybird larvae fed either a bean or pea aphid.

parametric estimates of the probability density function, to identify abrupt changes in the frequency of the inactivity durations. The kernel density estimates for the duration of inactivity revealed a distinct threshold at ~ 20 s (Fig. A.1).

The first bout of activity was divided into bouts of intensive and extensive search with a method based on the time spent in the vicinity of successive path locations, i.e., residence time [1]. Because intensive search is characterized by slow speeds and frequent turns, an animal searching intensively in an area will have a high residence time in that area. The residence time is an extension of the first passage time [2], which consists of the time spanning from when an animal entered and exited a virtual circle centered on a path location (Fig. A.2). The residence time algorithm extends the first passage time by allowing the animal to re-enter the virtual circle, which makes the residence time less sensitive to the choice of radius for the virtual circle than the first passage time [1]. Thus, the residence time represents the total time that the animal spends in the virtual circle (Fig. A.2). However, when an animal's

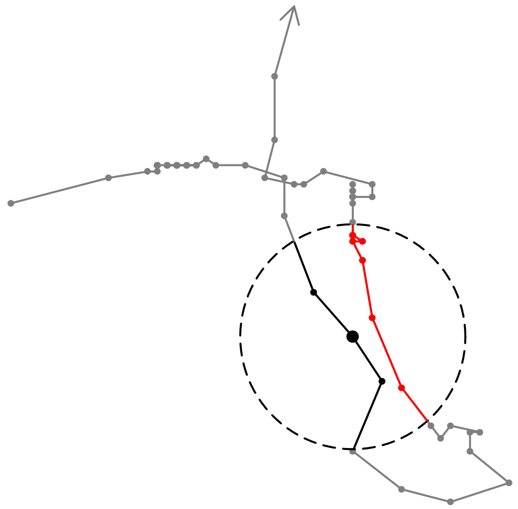

Figure A.2: Illustration of first passage time and residence time. The first passage time consists of the time spanning from when an animal entered and exited (black portion of path) a virtual circle (large dashed circle) with a fixed radius (5 mm) centered on a single location (large black dot). The residence time includes the total time spent in the virtual circle (black and red portions of path) by allowing for brief forays (≤ 10 s) outside of the circle, but the time spent outside of the circle is not included in the residence time. The locations in the movement path (small dots) are equidistant in time but not space (i.e., speed is not constant).

movements are confined to an experimental arena, or a central place such as a nest or burrow, the animal may exit and re-enter the same virtual circle many times and the total time spent in the virtual circle may consist of separate behavioral bouts. Therefore, the residence time algorithm allows for a constraint to be placed on the the amount of time that an animal may spend outside of the virtual circle.

We selected a small radius for the virtual circle (5 mm; $\approx 1/3$ of predator body length) and a low threshold for time spent outside of the virtual circle (10 s) because we had high-resolution data (1 location/s) for a slow-moving animal (mean speed = 1.1 mm/s) covering a small spatial extent (mean leaf area = 48 cm^2). We applied the residence time algorithm to (x,y)-coordinates that are equidistant in time but not

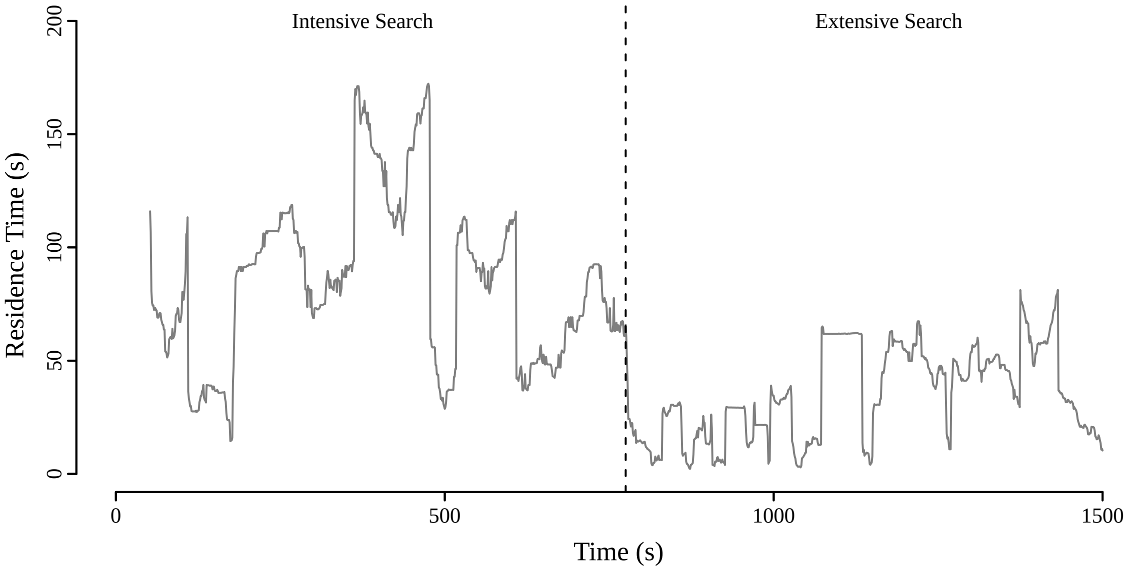

Figure A.3: Illustration of a residence time series. A statistical method was used to divide the residence time series into bouts of intensive and extensive search.

space (i.e., speed is not constant). Thus, our analysis focused on changes in movement behavior over time rather than space. This allowed us to identify the duration of behavioral bouts rather than the more typical usage of identifying space-use behavior [1].

The residence time was calculated for each (x,y)-coordinate along the movement path, which produced a residence time series (Fig. A.3). The residence time series provided a signal of how intensively the predator uses space over time. The challenge was to objectively divide the signal into bouts of intensive and extensive search. We used a method that statistically divides the signal to find the most likely breakpoints in the residence time series [3, Fig. A.3]. The method finds breakpoints relative to the magnitude of the highest value in the signal. Thus, there was not a single, absolute value of residence time that was indicative of intensive search across all individuals.

A.1 References

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Appendix B

Detailed Model Description

B.1 Search behavior

Search behavior was modeled with Lévy walks; random walks with move lengths selected from a Pareto power-law probability distribution and headings drawn from a uniform distribution. The probability of moving a distance of length l is given by $p(l) \sim l^{-\mu}$ with $1 < \mu < 3$. Different values of μ produce different strategies. As $\mu \to 1$, the resulting random walk becomes ballistic motion and the forager travels in a straight line until it reaches a resource or the landscape boundary. For $\mu \geq 3$, the distribution of move lengths has finite variance, and by the central limit theorem, the resulting random walk converges to Brownian motion at sufficiently large temporal and spatial scales.

Foragers moved incrementally along a heading at a constant speed (0.25 units/time step). At each time step, the forager checked for resources in its immediate vicinity (detection radius = 0.5 units). If the forager moved the distance specified by the move length without detecting any resources, then a new heading and move length were drawn. Upon detecting a resource, the forager changed its heading to move directly toward the resource (i.e., move lengths were truncated by resource encounters). When the forager reached the resource, it stayed in that location for a single time step to consume the resource (handling time = 1 time step) before drawing a new heading and move length. Resources were not replaced or renewed during a run of the simulation.

Foragers moved according to composite random walks and switched between extensive and intensive search modes. Each search mode was characterized by a parameter specifying the move length distribution (μ_{ext} and μ_{int}). We examined two criteria for determining when to switch between search modes: giving-up time and giving-up density. For the giving-up time strategy, the forager engaged in intensive search until the time since last resource encounter exceeded the giving-up time. For the giving-up density strategy, the forager set its search mode to intensive if the resource density exceeded the giving-up density. We calculated a generalized measure of local resource density, $f(x)$, by summing the contribution of each resource, r_i, from the set of all resources, R, on the foragers location, x, weighted by distance according to a normal distribution.

$$f(x) = \sum_{r_i \in R} \frac{1}{\sqrt{2\pi}\sigma} \exp(-\frac{\parallel x - r_i \parallel^2}{2\sigma^2})$$

In all simulations, the standard deviation, σ, was set to 1.

B.2 Resource distribution

Resources were distributed across the landscape according to a Neyman-Scott process, which provides a mechanistic model for the aggregation of resources and is one of many spatial point processes that can produce negative binomial distributions [1]. The algorithm involved randomly drawing the number of resource aggregations, or clusters, from a Poisson distribution with an expected value of 15 (Table 3.1). The center of each cluster was randomly assigned to a point in the landscape (i.e., parent point). Then resources were sequentially assigned to a random parent and randomly placed within a specified radius (i.e., cluster radius) of the parent point until all resources were distributed among the parents. Thus, for each run of the simulation, the algorithm randomly determined the number of clusters and the number of resources per cluster, but the initial total resource density and the cluster radius were fixed. By changing a single parameter (i.e., cluster radius), we were able to vary the aggregation of resources, which ranged from tightly clumped (cluster radius = 4) to dispersed (cluster radius = 64)

B.3 Landscape properties

Because the choice of the landscape boundary condition is critical for modeling animal movement, we briefly overview the main types of boundary condition (i.e., reflecting, periodic, absorbing) to provide justification for our choice. Foragers may respond to a boundary by reflecting back into the landscape. However, reflecting off the landscape boundary introduces directionality of movement into our random search framework and introduces the directionality in an artificial way because of the abrupt geometric boundaries in the simulated landscape. In a periodic boundary, the top/bottom and left/right of the landscape are wrapped to create a torus-like surface (i.e., forager exits on one side of landscape and re-enters on opposite side). When resources are not depleted, or renew quickly relative to the speed of the forager, the periodic boundary condition simulates an infinite landscape. However, when resources are depleted without renewal, as in our model, the periodic boundary condition simulates a new forager entering the landscape. The new forager, therefore, always enters the landscape at the boundary, which introduces the possibility of boundary artifacts. In our model, we used an absorbing boundary where a forager that encountered the landscape boundary was placed randomly back into the landscape. Alternatively, we could have removed the forager from the landscape after encountering the boundary, thereby terminating that run of the simulation. However, early termination of a simulation would have reduced the effect of resource depletion.

In the model, space was continuous, i.e., the spatial coordinates of the resources and forager were floating-point numbers. The core area of the landscape (101 x 101 units) was surrounded by a buffer of 5 units on all sides yielding a total landscape area of 111 x 111 units. The buffer did not contain any resources and allowed a forager that encountered a resource at the edge of the core area to engage in intensive search without immediately leaving the landscape.

B.4 Parameter sweep and optimization

We used a grid-based search to explore the searching efficiency associated with large regions of the parameter space of our simulation model. We examined 4 initial resource densities, 5 cluster radii, 2 search strategies (GUT and GUD), and 11 values for each searching parameter (μ_{ext}, μ_{int}, switching threshold; Table 3.1). In the first sweep of the parameter space, we conducted 100 runs for each parameter combination for a total of 5,3240,000 runs (4 densities x 5 radii x 2 strategies x 11^3 search parameters x 100 runs). Each run of the model consisted of 20,000 discrete time steps, which was a sufficiently long duration to ensure that resource depletion was adequate. Because non-composite search strategies provide a baseline for comparison with the composite search strategies, we also collected data on the performance of a non-composite search strategy (i.e., Lévy walk with one μ parameter) in each landscape for an additional

110,000 runs (4 densities x 5 radii x 11 μ values x 500 runs).

The full grid-based search produced a rough fitness surface based on the searching efficiency of each parameter combination. The fitness surface allowed us to exclude regions of the parameter space that led to poor searching efficiency, thereby focusing our computational resources on increasing replication in regions of the parameter space that were likely to contain the optimal parameter combination. We used an iterative process (described below) to narrow the regions of the parameter space selected for increased replication. The iterative process did not produce a finer-scale resolution of the parameter space but rather increased the replication for subsets of the parameter combinations used in the full grid-based search (Table 3.1). Within each landscape type, we used the mean searching efficiency (resources consumed/total distance moved) from the full grid-based search to select the top 13 of the 1,331 (1%) possible parameter combinations. Within that 1%, we used the range of values for each parameter to reduce the parameter space. For some landscape types, this approach did not reduce the parameter space substantially. Thus, we conducted 200 runs for each parameter combination in the reduced parameter space and again calculated the top 1% of the parameter combinations to further reduce the parameter space. This process was repeated until the optimal parameter combination was comprised of at least 500 runs because preliminary exploration of the model indicated that 500 runs produced good estimates of mean searching efficiency.

B.5 References

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Appendix C

Supplementary Figures

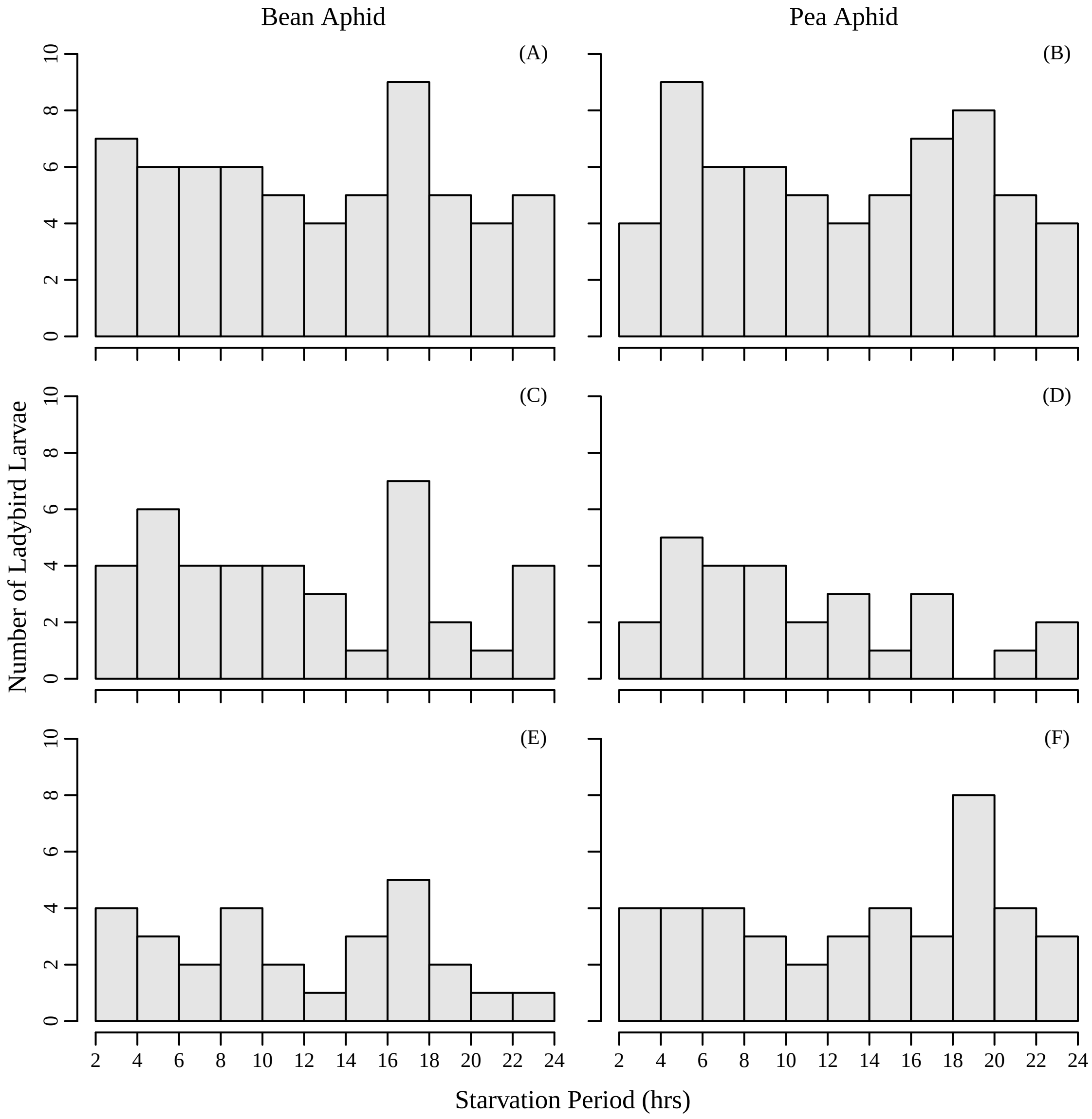

Figure C.1: Distribution of starvation periods for behavioral trials with ladybird larvae. We fed ladybird larvae either a single bean or pea aphid and then measured the time spent engaged in several different behaviors: (A-B) handling & post-handling time (same distribution for both behaviors), (C-D) inactive time, and (E-F) intensive search time. See Chapter 2 for additional details.

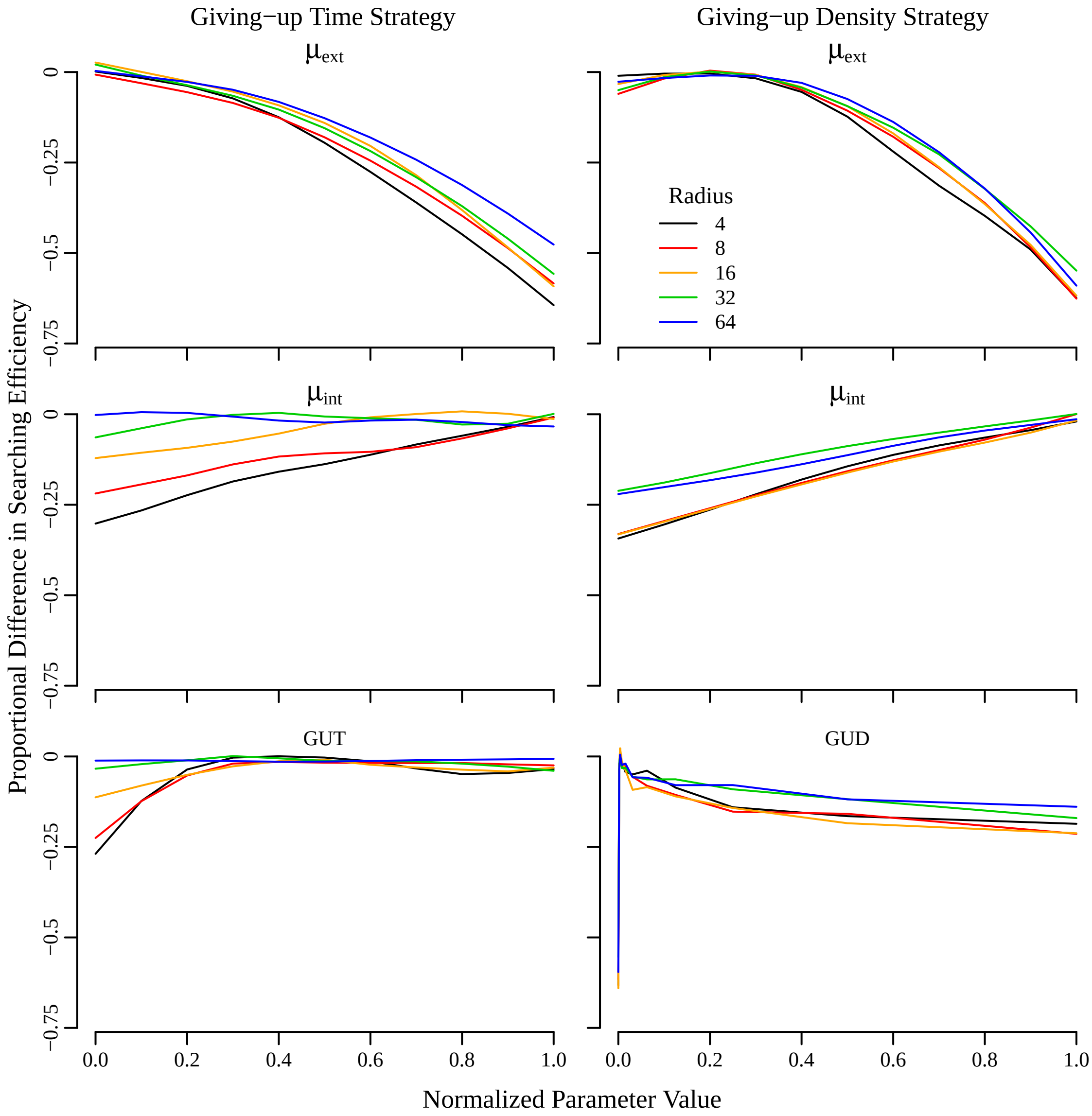

Figure C.2: Sensitivity of searching efficiency to the three parameters associated with two different composite search strategies (resource density = 100). Parameter values were normalized for comparison. See Chapter 3 for additional details.

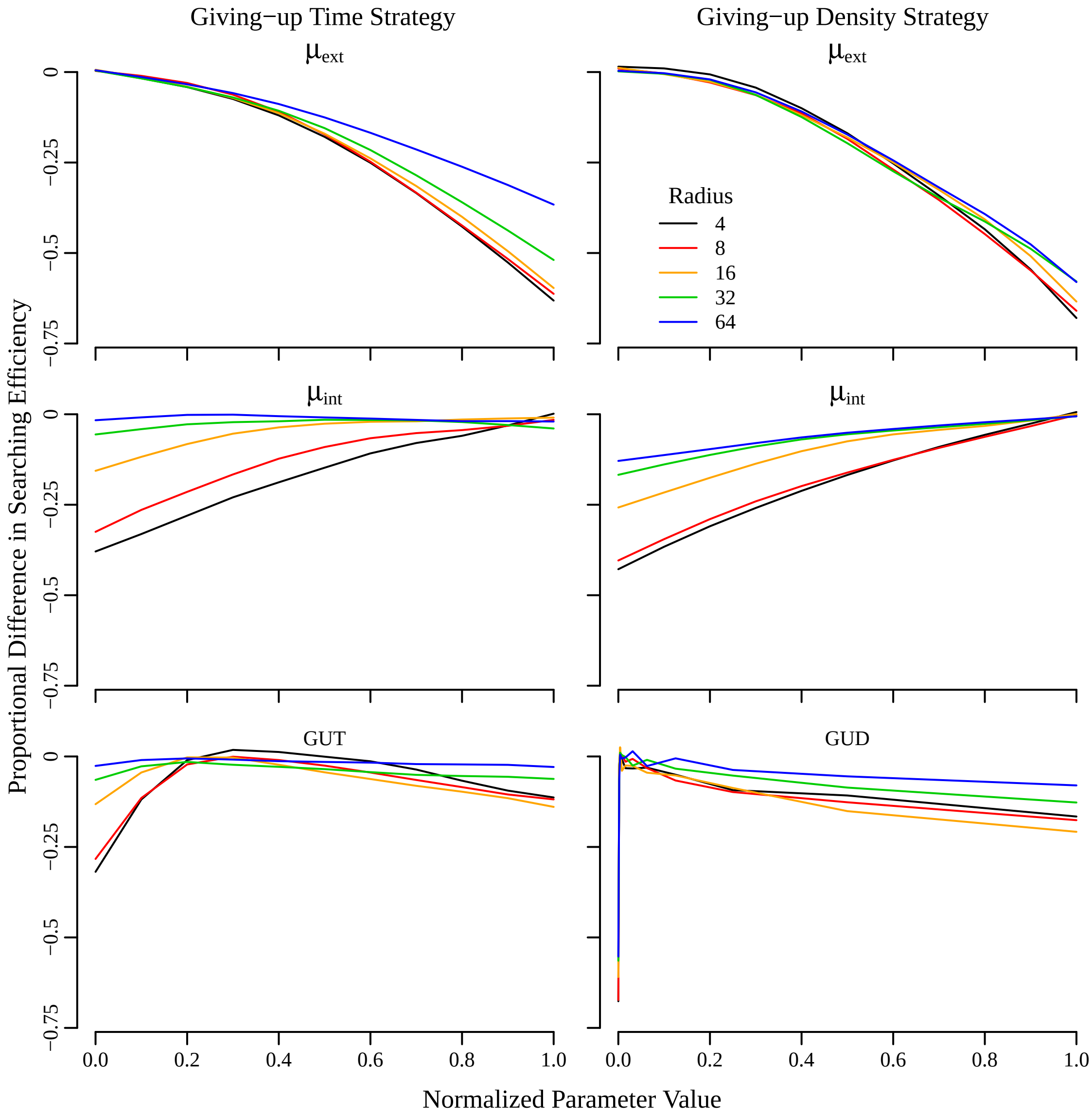

Figure C.3: Sensitivity of searching efficiency to the three parameters associated with two different composite search strategies (resource density = 400). Parameter values were normalized for comparison. See Chapter 3 for additional details.

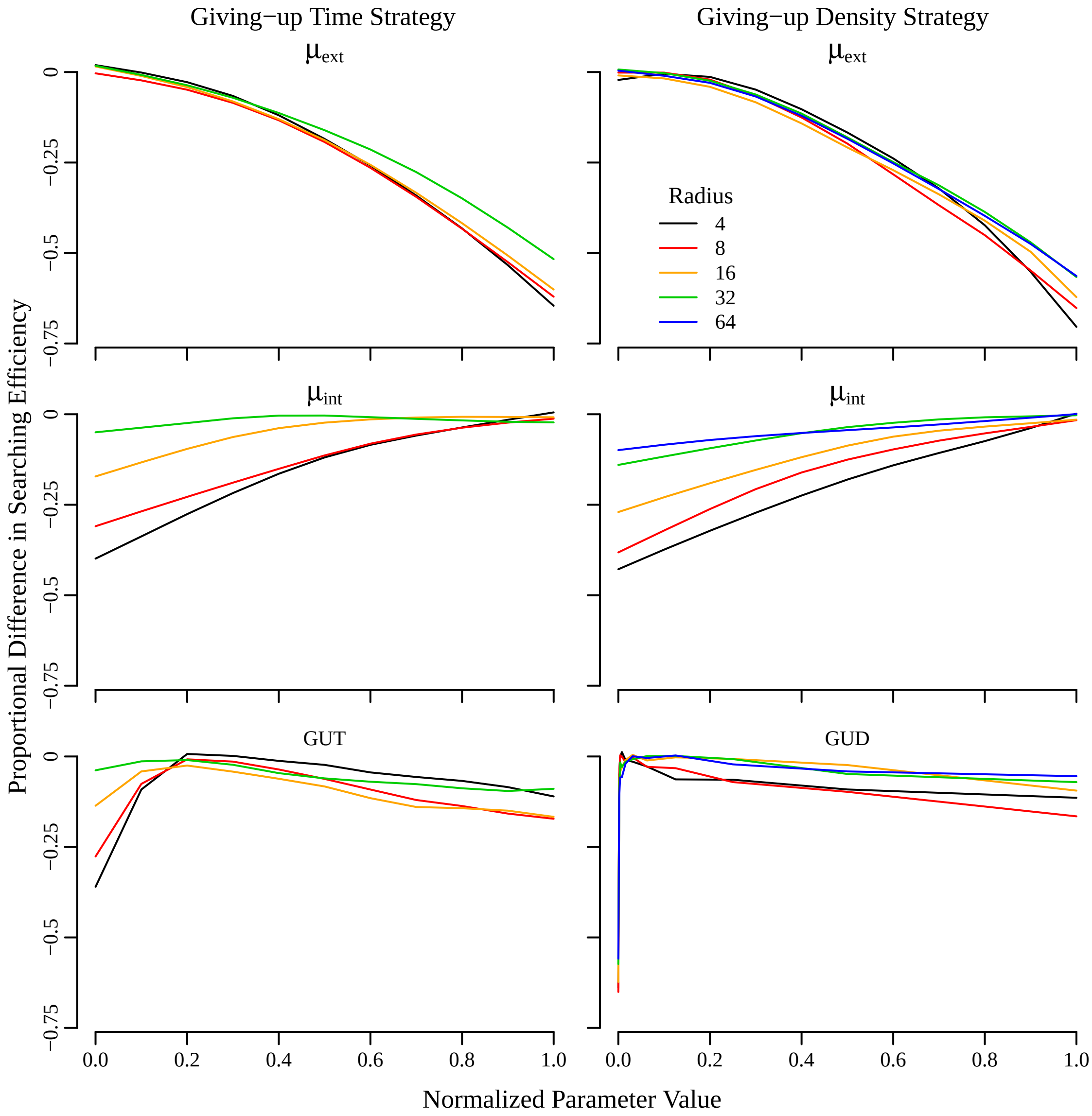

Figure C.4: Sensitivity of searching efficiency to the three parameters associated with two different composite search strategies (resource density = 700). Parameter values were normalized for comparison. See Chapter 3 for additional details.

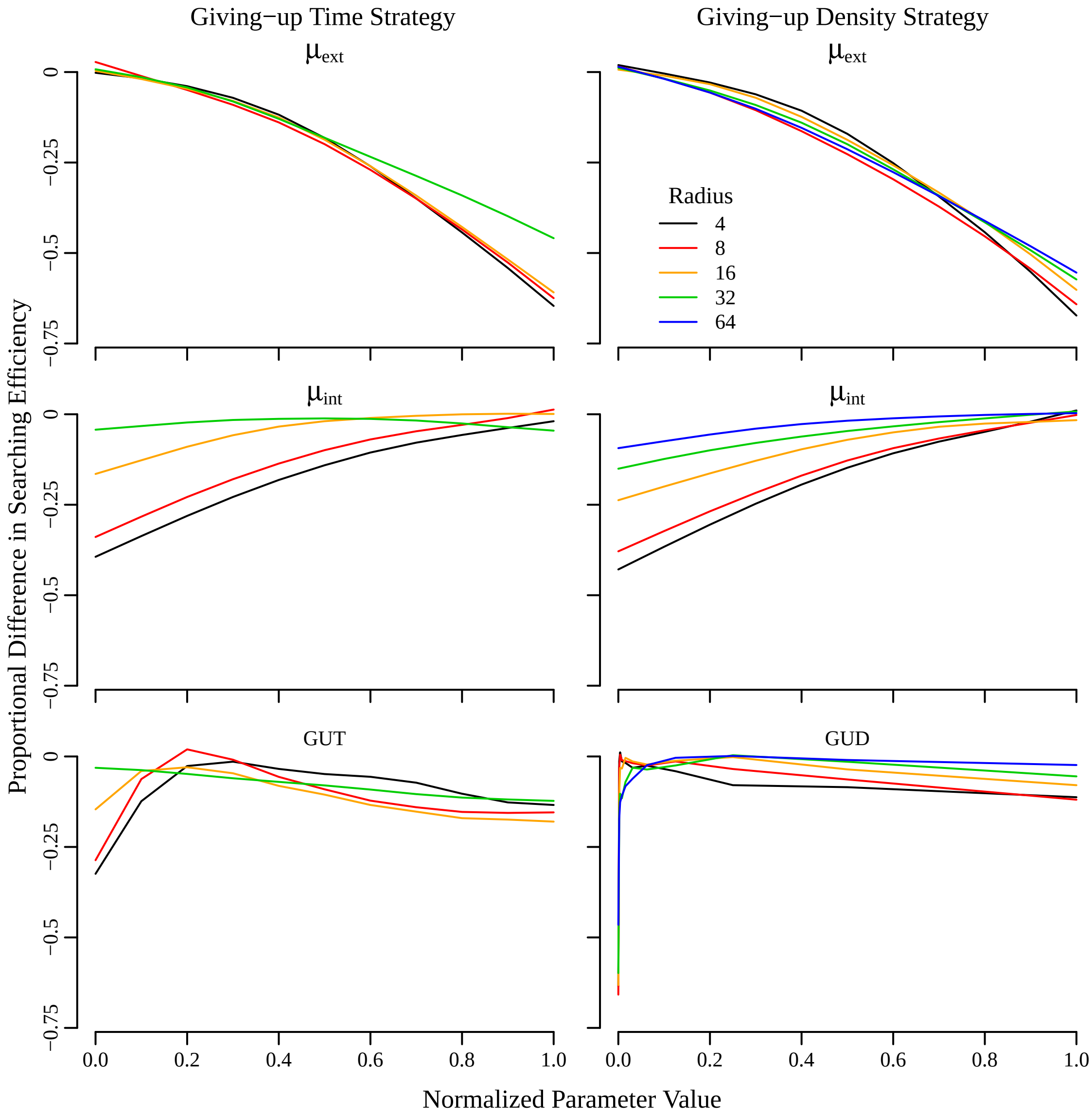

Figure C.5: Sensitivity of searching efficiency to the three parameters associated with two different composite search strategies (resource density = 1000). Parameter values were normalized for comparison. See Chapter 3 for additional details.

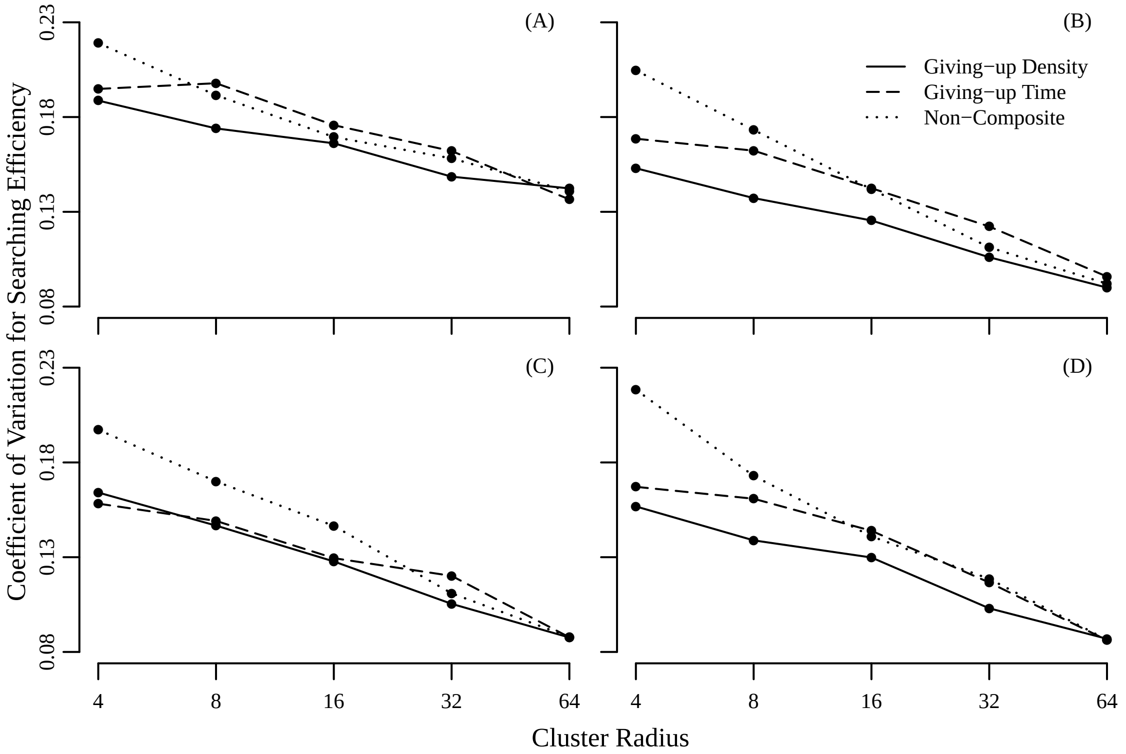

Figure C.6: Coefficient of variation in searching efficiency for three search strategies across 5 levels of resource aggregation and 4 levels of resource density: (A) 100, (B) 400, (C) 700, (D) 1000. Resource aggregation decreases with increasing cluster radius. The x-axis is presented on the $\log_2$ scale. See Chapter 3 for additional details.

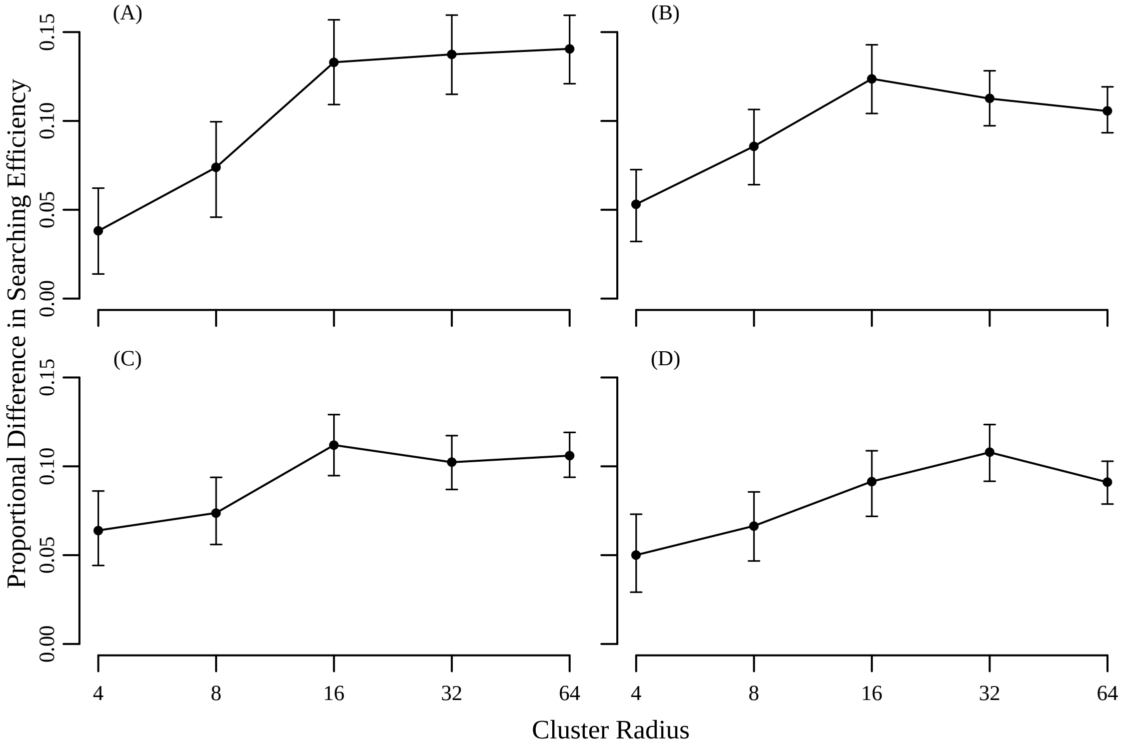

Figure C.7: Effect of resource aggregation on proportional difference in searching efficiency, D_{G}, between giving-up time and giving-up density strategies across 5 levels of resource aggregation and 4 levels of resource density: (A) 100, (B) 400, (C) 700, (D) 1000. The proportional difference was calculated as $D_{\mathrm{G}} = (\bar{y}_{\mathrm{GUD}} - \bar{y}_{\mathrm{GUT}})/\bar{y}_{\mathrm{GUT}}$, where $\bar{y}_{\mathrm{GUT}}$ and $\bar{y}_{\mathrm{GUD}}$ were the mean searching efficiency of the giving-up time and giving-up density strategies, respectively. Points represent the mean proportional difference in searching efficiency between the two search strategies and error bars represent 95% quantiles of the bootstrapped data set. Resource aggregation decreases with increasing cluster radius. The x-axis is presented on the $\log_2$ scale. See Chapter 3 for additional details.