

Bio-inspired Role Allocation of Heterogeneous Teams in a Site Defense Task



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Abstract We consider here the use of heterogeneous UAV swarms to defend a high-value target. We gain inspiration from the guarding system used by colonies of *Tetragonisca angustula* bees, which uses both high-cost hovering guards and low-cost standing guards to protect within-nest resources from theft by their own and other species (con- and heterospecific invaders, respectively). Hovering guards discern heterospecifics from conspecifics, and standing guards discern conspecific invaders from nestmates. Using a value-based multi-agent simulation, we find that, when heterospecific invaders deduct much more value from the defended resources than conspecifics, a heterogeneous defense force preserves value most effectively. Consequently, when facing heterogeneous invaders, focus should be on building effective mixtures of heterogeneous defensive agents instead of enhancing capabilities of homogeneous robotic swarms. Our results also contribute to better understanding *T. angustula*'s guarding system.

1 Introduction

We are interested in the problem of defending a secured location, or High-Valued Target (HVT), against swarms of expendable adversarial UAV agents, particularly by using a swarm of defensive UAV agents. A similar problem for mobile robots was explored in [7, 8], in which a team of defending robots attempts to deter simple attacker robots from entering a specified region of a horizontal playing field. In contrast to the problem discussed in [7, 8], in which all defending robots could

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counter all individual attackers equally effectively, we investigate the more complex problem of two types of attackers, each type of which can only be detected by one of two types of sensor, with defender robots equipped with one enemy-detecting sensor each. By not equipping an entire defending swarm of agents with the sensors necessary to detect both types of attackers, the heterogeneous swarm of defenders is then likely less costly to build than a heterogeneous swarm of the same size with each agent having both sensors.

In particular, consider the case in which one sensor type (and therefore one agent role) is more expensive than the other; the cost of such a heterogeneous swarm is then a function of not only the expected size and constitution of the adversarial force and the total number of defenders required to successfully defend the HVT, but also on the number of expensive agents required. With such a scenario in mind, we present here our investigation of an approach for determining the appropriate allocation of UAVs to two different guarding roles to defend an HVT against an enemy swarm comprised of two different types of enemy UAVs, cast in a utility-maximization framework.

In our approach, we draw inspiration from biology, specifically the allocation of guard bees to guarding roles in colonies of *Tetragonisca angustula* stingless bees in their efforts to defend their nests and the valuable resources within from invading bees of both the same species (conspecific invaders) and other species (heterospecific invaders).

It is important that bees both safeguard and make wise usage of the resources stored in their nest to ensure the colony's continuing prosperity. Those resources include not only food for the colony, but also the bees themselves, which are required not only for guarding the nest but also for in-nest activities related to the long-term health of the colony. Consequently, it may be beneficial not only for bees to maintain effective defenses against invaders, but to do so using the smallest defensive force that is best matched to expected challenges.

Role allocation on a team is an important consideration in several domains. In the operations research literature, we see examples for allocating workers with varying capabilities to job roles. A notable example of this is in [5, 15], in which an integer programming formulation is used for the scheduling of two classes of bank employees based on the expected volume of work and the expected quality of work performed by each employee type. In multi-robot teams, the proper allocation to roles could be dynamic. In [9], Emery, Sikorski, and Balch consider how to dynamically allocate robots to roles in a robot team, and in [16], Martison and Arkin consider how individual robots on a team can learn when to switch from one role to another to best support the team's objectives. Our work approaches a similar problem: that of scheduling UAVs to guarding roles in a site defense task.

In this paper, we are concerned with the allocation of robots with varying sensor capabilities and costs to a site defense task, where the cost of invaders can vary. Section 2 provides biological background on these guarding specializations utilized by *T. angustula*. In Sect. 3, we define the scenario under investigation in a manner suitable for simulation. Section 4 contains the analysis of these simulations, followed

in Sect. 5 by a brief discussion on extensions for practical application of the results. Finally, Sect. 6 presents conclusions and thoughts on future work in this area.

2 Biological Motivation

In this section, we consider the biological background and motivation from the literature and from recent field experiments involving *T. angustula* stingless bees. A *T. angustula* nest contains valuable resources that the colony needs to safeguard in order to survive and prosper. To protect these resources, *T. angustula* colonies have two types of guard bees: hovering guards and standing guards [18]. Hovering guards, which specialize in identifying heterospecific invaders [14], hover in a specific formation in front of and to the sides of the entrance tube, possibly orienting themselves in such a way that they have a clear view of any insects approaching the nest entrance [18]. As hovering guards identify intruders via visual differences from their own species, they cannot easily discern nestmates from conspecific non-nestmates [2]. Standing guards fill this role; they stand stationary on the nest's entrance and examine any bees attempting to crawl into the entrance tube via antennal contact, allowing them to determine whether or not the bee is a nestmate [13, 14]. Both types of guards will attempt to deter—and if necessary, injure or kill—any detected intruder, though possibly at the cost of its own life [12, 14, 18]. *T. angustula* is a particularly interesting study with regards to role allocation, as its species is unique in concurrently maintaining these two distinct sets of guards; most other bee species that guard their nests with a single set of guards standing at or near the entrance [10, 14, 17–19].

Field observations of *T. angustula* suggest that a minimal team of guards trades guarding responsibilities continuously and is reinforced by additional bees from within the colony as needed. In a different study by one of the authors of this paper [1], *T. angustula* guards were observed over the course of three days to have a 27.7% chance of switching which guarding task they performed from one day of observation to the next. Furthermore, a second experiment was conducted that tested the colony's response to the continual removal of hovering and standing guards. Over a period of several hours, a total of eighty-eight guards were removed. After each phase of guard removal, both types of removed guards were readily replaced by the colony, which indicates that both types of guards are valued equally by the colony.

Grüter, Kärcher, and Ratnieks [10] suggest that colonies may employ more standing guards at a given time than hovering guards due to the standing guard role being less energetically taxing than hover-guarding for the colony. They also postulate, alternatively, that the employment of more standing guards than hovering guards in the colonies they observed could have been motivated by the colonies being under more frequent threat of conspecific robbery than heterospecific. Both of these suggestions seem plausible not only for stingless bees but for heterogeneous swarms of defensive UAVs, and we investigate them both in multirotor UAV simulations described in Sect. 3.

3 Simulation

We constructed a simulated UAV site-defense task inspired by the observations of the interactions among standing guards, hovering guards, conspecific intruders, and heterospecific intruders in *T. angustula* stingless bees. Our goal was to use simulation to investigate how the optimal allocation of guards—both in amount and type—is affected by the potential cost of an invasion—that is, how many invaders of each type are present and how much value each can individually remove from the “nest.”

Our simulations were performed in SCRIMMAGE, a multi-agent robotics simulator [3, 4], and the motion of each UAV was modeled with simple quadrotor dynamics. We chose quadrotor parameters to be consistent with scaled bee flight dynamics, which allows us to model the entities in simulation using stingless bee energy expenditure characteristics. We performed thousands of Monte-Carlo simulations in SCRIMMAGE in which we varied invader costs, invader type distributions, and guard role distributions. Figure 1 is a screenshot captured from one of these simulations and shows hovering and standing guard UAVs, conspecific and heterospecific invader UAVs, and the High-Value Target (HVT) nest.

Each simulation is initialized with up to ten of each of the four types of UAV – hovering guards, standing guards, conspecific intruders, and heterospecific intruders. Guards are generated at random positions within specific bounds to mimic their biological counterparts. Hovering guards are positioned to either side of the front of the HVT entrance. Standing guards are placed around the HVT entrance itself in a cylindrical formation. Details of guard sensing characteristics are discussed in Sect. 3.2. Invaders are initialized far away from the nest and guards and initially perform random walks where the guards cannot sense them. Every 60 s of simulation time, a randomly selected invader approaches the nest, following waypoints that ensure it will be seen by both sets of guards.

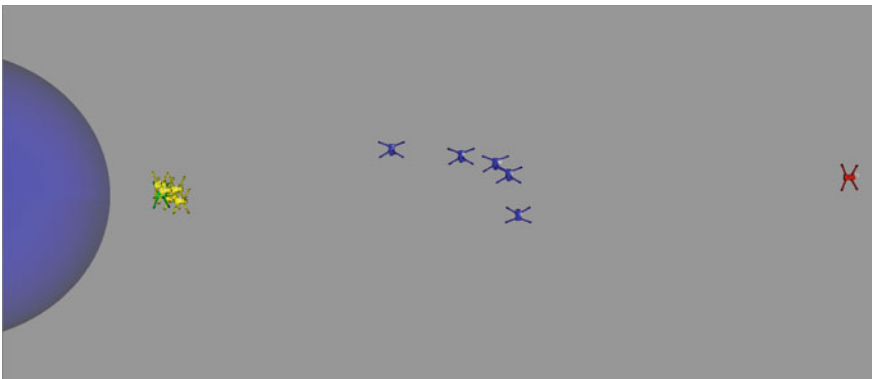


Fig. 1 Screenshot of an example simulation run. Blue UAVs are hovering guards, yellow UAVs are standing guards, the green UAV is a conspecific invader being investigated by one of the standing guards, and the red UAV is a heterospecific invader

Table 1 Value-Related Parameters

	Parameter	Value
Hovering	Caloric burn rate	1.250 $\mu\text{cal/s}$
	Average guard time	3420 s (57 min)
	Initialization cost	4275 μcal
Standing	Caloric burn rate	0.250 $\mu\text{cal/s}$
	Average guard time	4440 s (74 min)
	Initialization cost	1110 μcal
Heterospecific	Breakthrough penalty	5000, 10000, 15000 μcal
Conspecific	Breakthrough penalty	4275 μcal

The value contained within the HVT is denoted by \mathcal{V} , which is analogous to the resources inside a *T. angustula* nest. Both \mathcal{V} and the guards' energy levels are measured in units of μcal . \mathcal{V} is initialized to 100000 μcal , which allows for initialization of the maximum number of each type of guard plus generous margin. When each guard is initialized, a set amount of μcal is deducted from \mathcal{V} to refuel the guard; this quantity, referred to as the guard's initialization cost, is the guard's initial energy level, and also defines the guard's maximum energy level. Any intruders that reach the nest subtract a breakthrough penalty from \mathcal{V} . These guard initialization costs and invader breakthrough penalty cost levels are provided in Table 1. For heterospecific invaders, simulations were run for breakthrough penalties of 5000 μcal , 10000 μcal , and 15000 μcal to allow us to investigate the impact of different levels of heterospecific attack effectiveness on the guards' ability to survive and defend the HVT. Conspecific invader breakthrough penalty was held constant at 4275 μcal . Each combination of number of hovering guards, number of standing guards, number of heterospecific invaders, and number of conspecific invaders was run in simulation 100 times at each level of heterospecific breakthrough penalty. The initial cost of each of the guard roles is derived from metabolic rate estimates from Duell et al. [6] and on the average amount of time each guard type was observed to perform its duties by Grüter et al. [10]. To represent the exhaustion of each guard's energy levels over time, each guard's energy level decays at the rates specified in Table 1, and any guard whose energy level reaches zero is removed from simulation.

During each timestep of the simulation, each guard checks its energy level and then searches within its sensing range and field of view (FOV) for any targets of interest. Guards select a target to engage and succeed (and survive) with a set probability. Although guards are sensitive to their own energy level, neither guards nor intruders are aware of the current value of \mathcal{V} , and thus all of the steps of the invaders' attacks and the guards' defensive actions are independent of the current value of \mathcal{V} . The steps taken by each guard during each timestep of simulation are described in greater detail in the remainder of this section.

Table 2 Guard Sensing Distances

	Guard type	
	Standing (m)	Hovering (m)
Sensor range	5	15
Engagement range	2	5

3.1 Energy Check

At the beginning of each timestep, each guard checks its internal energy level, which is presented in terms of percent of energy remaining from the full level. As the simulation progresses, guards with lower levels of energy remaining are more likely to return to the HVT to refuel from the HVT's remaining value. Refueling guards stay in the HVT only briefly, as a UAV's refueling is assumed to occur instantaneously once its centroid comes within the HVT's boundary. Once refueled, guards return to their previous position to continue guarding in the same role as before.

3.2 Sensing

Guards are limited in the invader UAVs they may engage based on their sensing capabilities. To reflect their greater mobility, hovering guards can sense and engage enemies at longer distances than standing guards; these distances are defined in Table 2. Within their respective sensing ranges, both types of guards can sense UAVs whose centroids are within $\pm 45^\circ$ of their frontward centerline, as illustrated in Fig. 2.

3.3 Evaluation and Target Selection

Either guard type can attack either type of enemy. As an adversary passes within the sensing range of a guard's FOV, the guard decides whether it is or is not a candidate for attack. To represent the primary foci of hovering and standing *T. angustula* guards detailed in Sect. 2, in this simulation, hovering guards specialize in identifying only heterospecific invaders, and standing guards focus only on identifying conspecific invaders. The probabilities of each type of guard identifying a member of each invader type as an attack candidate, p_{AC} , are defined in Table 3. Each guard independently decides which UAVs in its FOV are attack candidates; guards do not share this information with each other. Of a guard's detected attack candidates, it selects one to target from a uniform random distribution.

Fig. 2 Diagram illustrating a guard UAV's FOV. The leftmost UAV can sense the blue UAV but not the red UAV

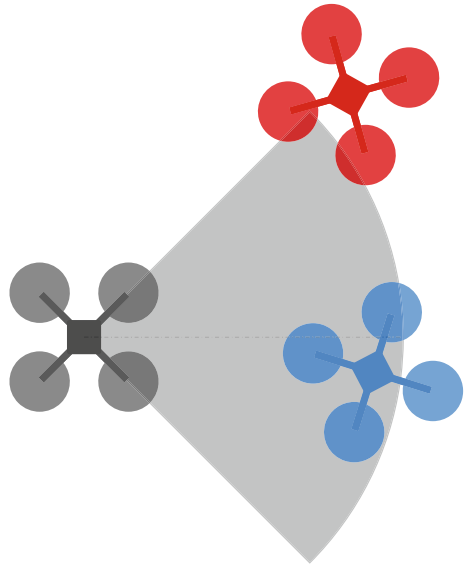


Table 3 Threat Discernment Probabilities

Guard Type	Invader type	p_{AC}
Standing	Heterospecific	0.01
	Conspecific	0.99
Hovering	Heterospecific	0.99
	Conspecific	0.01

3.4 Target Pursuit and Engagement

If a guard's selected target is not within engagement range, the guard pursues it until the target either enters the HVT, is killed by another guard, or comes within engagement range, at which point the pursuing guard attempts to engage it. As standing guards are the HVT's absolute last defense, we assume for simplicity that once a UAV has survived any encounter with a standing guard, it is close enough to the HVT entrance to enter unhindered. Thus, a guard engages its target if the target: (1) is not already engaged, and (2) has not yet been in an engagement with a standing guard. A guard that engages an enemy and survives the encounter may then engage another incoming intruder. Likewise, an invading UAV that survives an engagement with a hovering guard may then become embroiled in a subsequent engagement, either with the same guard (if it survived) or another.

During each simulation timestep in an engagement between a guard and an invader, the probability of the engagement continuing for another timestep is 0.99. This ensures that most engagements last for several seconds or even minutes of

simulation time, echoing the wrestling between *T. angustula* guards and would-be intruders [11]. While the intruder in the engagement cannot make further progress towards the HVT entrance while engaged, the guard is also fully occupied with its opponent and cannot sense any other incoming intruders, leaving the colony more vulnerable to attack. Each UAV has a 50% chance of surviving the engagement, which is independent from its opponent's probability of survival. Consequently, each of the four outcomes (both surviving and disengaging, both dying, guard dying and invader surviving, guard surviving and invader dying) have an equal probability of 0.25.

If a guard survives an engagement, it returns to its initial position and begins to search for new invaders. If an intruder survives the guards and reaches the HVT, it deducts its type's breakthrough penalty (Table 1) from \mathcal{V} , then is removed from the simulation.

4 Results

Figure 3 summarizes the results for the low-threat case of two low-penalty, heterospecific invaders and two conspecific invaders over a variety of different guarding schedules. For this low-threat case, our simulation results suggest that the optimal defense strategy is to use only two standing guards. However, that case is not much better than the trivial solution of dispatching zero guards. Thus, when invasions are low risk, the metabolic cost of maintaining guards is worse than the losses to intruders.

Figure 4 shows the results for the moderate-threat case of three high-cost, heterospecific invaders and three conspecific invaders over the same selection of guarding schedules as in Fig. 3. Our simulation results suggest that the optimal guard schedule for this case is two hovering guards and two standing guards. However, a ridge emerges that creases around the line of two standing guards, and the decrease in the cost function for oversupplies of hovering guards is notably shallower than the decrease in the cost function for oversupplies in standing guards. Although hovering guards are significantly more costly in terms of energy, their ability to defend against costly heterospecific attacks may be driving this characteristic.

Figure 5 shows a high-threat case with eight moderate-penalty, heterospecific invaders and four conspecific invaders. Although the number of heterospecific invaders has increased, their individual penalties have been reduced. Thus, our simulations suggest that the optimal guard schedule is to deploy only two hovering guards and four standing guards. Due to the high total cost of invaders and the cost of maintaining any level of guard force, the maxima of \mathcal{V} in Fig. 5 are lower than in Figs. 3 and 4. The \mathcal{V} maximum in Fig. 5 occurs with two hovering guards and four standing guards. This proportion of hovering-to-standing guards is similar to the proportions observed by Baudier et al. [1] and Grüter et al. [10].

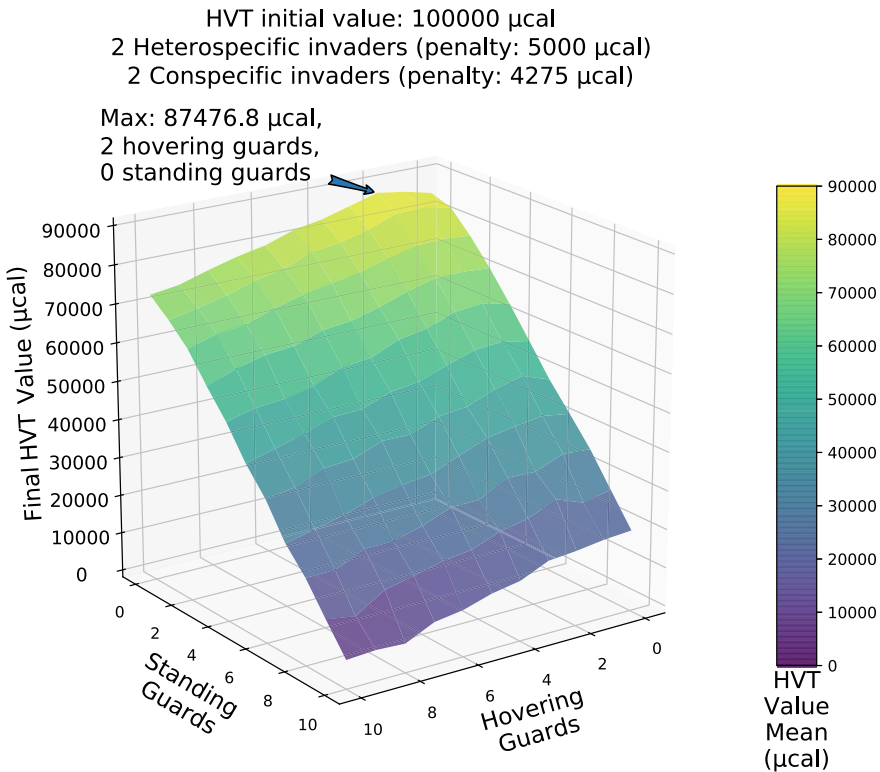


Fig. 3 Low-threat case. With heterospecific penalty set at 5000 μcal and with only two each of hetero- and conspecific invaders threatening the nest, few or no guards are required to preserve the hive’s value. Note that the maximum and the value at zero of each type of guard are nearly the same

5 Discussion: Reserves and Recruitment

Ultimately, if the cost of an enemy invasion can be accurately characterized in the same currency as the cost of defenses against those invasions (e.g., units of energy or fuel), then some invasions may be tolerated if they are rare and have limited scope. As stated in Sect. 3.1, guard UAVs in the simulations described in this paper are assumed to refuel instantaneously upon entering the HVT. We now drop this assumption to examine a more practical application of guard UAVs; given a scenario in which the desired allocation of guards to guarding roles is known, we wish to determine how many guards of each type are needed to maintain this desired guard schedule when guards with depleted energy must swap out with fully-fueled guards in order to themselves refuel. We define $t_{r,i}$ as the time a single guard of type i requires to refuel upon visiting the HVT, and $t_{g,i}$ as the amount of time the guard can spend performing its task after a full refueling. Let $N_{des,i}$ be the desired number of guards of type i for defending a particular HVT. To maintain $N_{des,i}$ guards defending

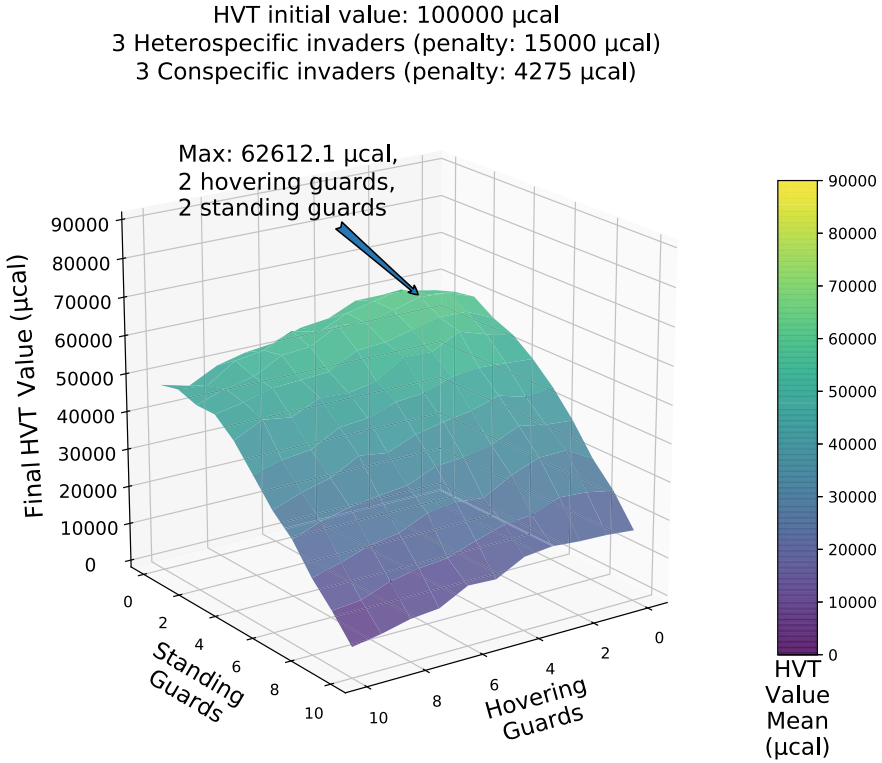


Fig. 4 Moderate-threat case. With heterospecific breakthrough penalty set to 15000 μcal , and with three each of hetero- and conspecific invaders attacking the HVT, \mathcal{V} is maximized with two hovering and two standing guards

the HVT for an extended continuous duration, $N_{req,i} > N_{des,i}$ guards are needed to allow for depleted guards to refuel, with $N_{req,i}$ defined as

$$N_{req,i} = N_{des,i} \left(1 + \frac{t_{r,i}}{t_{g,i}} \right).$$

If we assume that $t_{r,stand} = 30$ min, $t_{r,hover} = 22.5$ min, and $t_{g,stand} = t_{g,hover} = 45$ min, then to maintain a continuous guarding force of, for example, the maximizing combination of two hovering guards and four standing guards from Fig. 5 would require $N_{req,hover} = 6$, $N_{req,stand} = 10$. We note, however, that this method for computing $N_{req,i}$ assumes no guard attrition and is therefore a lower bound on the number of guards required.

In general, due to the logistical challenges of refueling and attrition, there are significant costs of guards beyond the variable costs of their operation. Maintaining a consistent guard force requires maintaining a consistent reserve force as well. Given these high costs of defense, it may be very important to ensure that a HVT is well

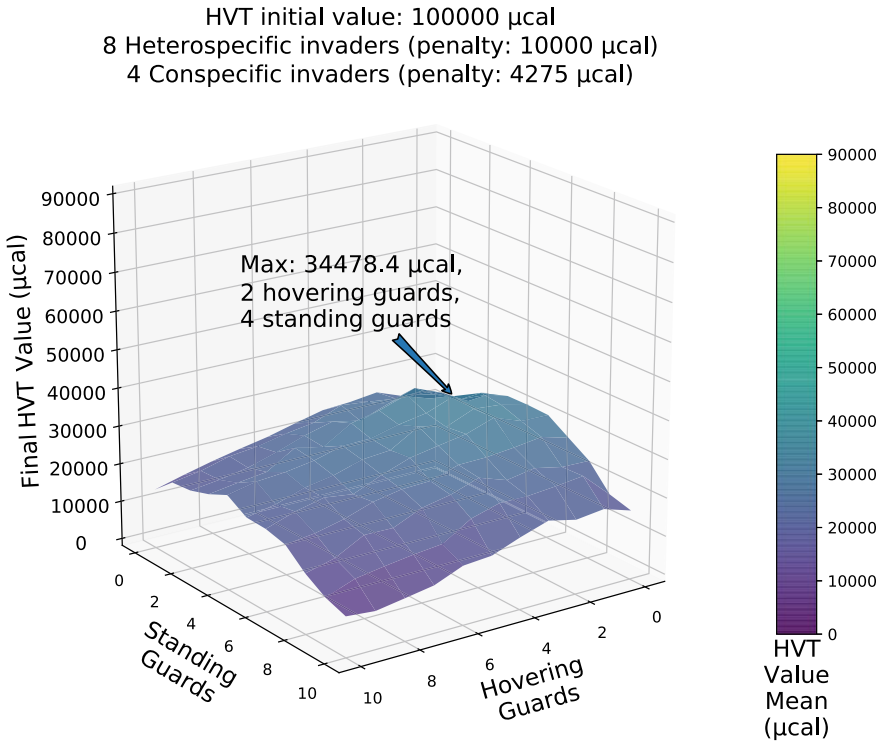


Fig. 5 High-threat case. The maximum \mathcal{V} for the case of heterospecific penalty of 10000 μcal , eight heterospecific invaders, and four conspecific invaders is achieved with two hovering guards and four standing guards. This is similar to the ratio of hovering-to-standing guards observed in nature [1, 10]

hidden in a cryptic environment so as to reduce the expected number of invaders. In natural *T. angustula* colonies, successful invaders could potentially recruit others on future invasion runs. Thus the high cost of guards and the maintenance of a persistent guard force may actually be a response to the risk (not modeled here) of future invasions from recruited invaders.

6 Conclusions and Future Work

In this paper, we presented a biologically-inspired scenario of a heterogeneous, multi-agent defense of an HVT facing potential invaders from a heterogeneous pool of adversaries. We used a simulation optimization approach to find the optimal guarding strategy in terms of net energetic cost to the HVT. In observations of *T. angustula* stingless bees, Grüter et al. [10] found that standing guards are a larger propor-

tion of the guarding force than hovering guards. The results from our simulation optimization approach are consistent with this observation, with lends support to the hypothesis that guard allocations are driven by the optimization of energy use. That is, as hovering guards require far more energy to deploy than standing guards, *T. angustula* colonies utilize more standing guards than hovering guards regardless of the frequency of heterospecific invasion attempts. As observed by Baudier et al. [1], however, hovering guards in *T. angustula* colonies are nonetheless important resources with numbers that are tightly regulated after removals. Thus, despite the numerical bias toward standing guards, the more costly hovering guards are still an important first line of defense. These observations coupled with the results of our simulation optimization approach suggest that, when defending a location against a heterogeneous group of adversary UAVs, a heterogeneous team of guard UAVs is better suited for defense than deploying teams consisting of only one type of guard.

In future work, we intend to more closely examine the dynamic role allocation problem briefly explored in Sect. 5 by incorporating guard “reserves” to be prepared to fill vacant guard roles, as well as modifying the simulation to allow guard UAVs to dynamically switch roles during an attack. Both of these offer great potential for a robust UAV defense of secure locations.

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References

1. Baudier, K.M., Ostwald, M.M., Pavlic, T.P., Pratt, S.C., Fewell, J.H.: Guard specialization in group defensive tactics of the stingless bee *Tetragonisca angustula* (2018). in preparation
2. Bowden, R.M., Garry, M.F., Breed, M.D.: Discrimination of con- and heterospecific bees by *Trigona (Tetragonisca) angustula* guards. *J. Kansas Entomol. Soc.* **67**(1), 137–139 (1994)
3. DeMarco, K., Squires, E.: SCRIMMAGE (Simulating Collaborative Robots In Massive Multi-Agent Game Execution), Aug 2017. <https://www.scrimmagesim.org/>
4. DeMarco, K., Squires, E., Day, M., Pippin, C.: Simulating collaborative robots in a massive multi-agent game environment (SCRIMMAGE). In: International Symposium on Distributed Autonomous Robotic Systems (2018)
5. Deutsch, H., Mabert, V.A.: Queuing theory and teller staffing; a successful application. *Interfaces* **10**(5), 63–67 (1980)
6. Duell, M.E., Roubik, D.W., Harrison, J.F.: Metabolic rate measurements of *Tetragonisca angustula* stingless bees, Jun 2017. Unpublished raw data
7. Earl, M.G., D’Andrea, R.: Modeling and control of a multi-agent system using mixed integer linear programming. In: Proceedings of the 41st IEEE Conference on Decision and Control, 2002, vol. 1, pp. 107–111. IEEE, Dec 2002
8. Earl, M.G., D’Andrea, R.: A study in cooperative control: the RoboFlag drill. In: Proceedings of the 2002 American Control Conference (IEEE Cat. No.CH37301), vol. 3, pp. 1811–1812. IEEE (May 2002)

9. Emery, R., Sikorski, K., Balch, T.: Protocols for collaboration, coordination and dynamic role assignment in a robot team. In: Proceedings of the 2002 IEEE International Conference on Robotics and Automation (Cat. No.02CH37292), vol. 3, pp. 3008–3015 (2002)
10. Grüter, C., Kärcher, M.H., Ratnieks, F.L.W.: The natural history of nest defence in a stingless bee, *Tetragonisca angustula* (Latreille) (Hymenoptera: Apidae), with two distinct types of entrance guards. Neotropical Entomol. **40**(1), 55–61 (2011)
11. Grüter, C., Menezes, C., Imperatriz-Fonseca, V.L., Ratnieks, F.L.W.: A morphologically specialized soldier caste improves colony defense in a neotropical eusocial bee. Proc. Nat. Acad. Sci. **109**(4), 1182–1186 (2012)
12. Jernigan, C.M., Birgiolas, J., McHugh, C., Roubik, D.W., Weislo, W.T., Smith, B.H.: Colony-level non-associative plasticity of alarm responses in the stingless honey bee *Tetragonisca angustula*. Behav. Ecol. Sociobiol. **72**(3), 58 (2018)
13. Jones, S.M., van Zweden, J.S., Grüter, C., Menezes, C., Alves, D.A., Nunes-Silva, P., Czaczkes, T., Imperatriz-Fonseca, V.L., Ratnieks, F.L.W.: The role of wax and resin in the nestmate recognition system of a stingless bee *Tetragonisca angustula*. Behav. Ecol. Sociobiol. **66**(1), 1–12 (2012)
14. Kürcher, M.H., Ratnieks, F.L.W.: Standing and hovering guards of the stingless bee *Tetragonisca angustula* complement each other in entrance guarding and intruder recognition. J. Apic. Res. **48**(3), 209–214 (2009)
15. Mabert, V.A.: A case study of encoder shift scheduling under uncertainty. Manag. Sci. **25**(7), 623–631 (1979)
16. Martinson, E., Arkin, R.C.: Learning to role-switch in multi-robot systems. In: 2003 IEEE International Conference on Robotics and Automation (Cat. No.03CH37422), vol. 2, pp. 2727–2734, Taipei, Taiwan, Sep 2003
17. Michener, C.D.: Notes on the habits of some Panamanian stingless bees (Hymenoptera, Apidae). J. N. Y. Entomol. Soc. **54**(3), 179–197 (1946). <http://www.jstor.org/stable/25005167>
18. Wittmann, D.: Aerial defense of the nest by workers of the stingless bee *Trigona* (*Tetragonisca*) *angustula* (Latreille) (Hymenoptera: Apidae). Behav. Ecol. Sociobiol. **16**(2), 111–114 (1985)
19. van Zweden, J.S., Grüter, C., Jones, S.M., Ratnieks, F.L.: Hovering guards of the stingless bee *Tetragonisca angustula* increase colony defensive perimeter as shown by intra-and inter-specific comparisons. Behav. Ecol. Sociobiol. **65**(6), 1277–1282 (2011)