

# Habitat features and performance interact to determine the outcomes of terrestrial predator–prey pursuits

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## Funding information

Australian Research Council, Grant/Award

Number: DP180103134; University of Queensland

Handling Editor: Laura Prugh

## Abstract

1. Animals are responsive to predation risk, often seeking safer habitats at the cost of foraging rewards. Although previous research has examined how habitat features affect detection by predators, little is known about how the interaction of habitat features, sensory cues and physical performance capabilities affect prey escape performance once detected.
2. To investigate how specific habitat features affect predation risk, we developed an individual-based model of terrestrial predator–prey pursuits in habitats with programmable features.
3. We ran simulations varying the relative performance capabilities of predator and prey as well as the availability and abundance of refuges and obstacles in the habitat.
4. Prey were more likely to avoid detection in complex habitats containing a higher abundance of obstacles; however, if detected, prey escape probability was dependent on both the abundance of refuges and obstacles and the predator's relative performance capabilities. Our model accurately predicted the relative escape success for impala escaping from cheetah in open savanna versus acacia thicket habitat, though escape success was consistently underestimated.
5. Our model provides a mechanistic explanation for the differential effects of habitat on survival for different predator–prey pairs. Its flexible nature means that our model can be refined to simulate specific systems and could have applications towards management programmes for species threatened by habitat loss and predation.

## KEYWORDS

conservation, ecology, individual-based, mammal, model, predation, refuge, survival

## 1 | INTRODUCTION

As being killed and eaten results in zero future fitness, habitats with high predation risk can exert strong selective pressure on the evolution of animal behaviour (Laundré et al., 2010). Many studies have examined how habitat features affect predation risk, typically focussing on how the amount of available cover affects the probability of being detected by predators (Dickman, 1992; Iribarren & Kotler, 2012; Myrsetrud & Østbye, 1999; Vásquez et al., 2002).

However, in nature, evading predation can be accomplished by two means: avoiding detection by a predator, and, if detected, succeeding in escape (Lima & Dill, 1990). Furthermore, although sensory cues such as vision, sound or olfaction may be sufficient to understand detection probability, escape success is determined both by sensory cues and relative performance characteristics related to the speed and manoeuvrability of the particular predator–prey pair. We currently lack a comprehensive framework that combines both sensory and performance characteristics to predict the total effect

of habitat features on predation risk. Understanding how different habitat features affect predation risk is not only fundamental in the study of predator–prey interactions, but it is also essential for identifying the full effects of habitat modification on threatened species and the underlying mechanisms that may be targets for improved conservation strategies (Didham et al., 2007; Doherty et al., 2015).

Animals rely on a range of sensory cues to detect nearby predators, prey and conspecifics. These cues can be visual, olfactory, auditory or tactile, and many animals make use of multiple cues simultaneously (Ilany & Eilam, 2008; Narins et al., 2005; Sündermann et al., 2008). Vision is one of the most frequently used sensory cues, particularly for pursuit predators which must keep track of a rapidly moving prey once the pursuit begins (Kane & Zamani, 2014; Lima & Dill, 1990; Mischiati et al., 2015). Consequently, certain habitat features can reduce the likelihood of detection by preventing sensory cues from being transmitted or received. One such feature is dense vegetative cover, which can make it difficult for a predator to detect prey and can thereby reduce predation risk (Dickman, 1992; Iribarren & Kotler, 2012; Mysterud & Østbye, 1999; Vásquez et al., 2002). For example, degu *Octodon degus* (a type of diurnal rodent) were more vigilant in open than shrub habitats (Vásquez et al., 2002), and Nubian ibex *Capra nubiana* had lower giving up densities in dense cover, even when foraging further from a refuge (Iribarren & Kotler, 2012). These results suggest that vegetative cover provides safety via concealment rather than as a refuge. However, while vegetative cover can reduce the chance of being detected by a predator, the reverse is also true—dense cover can make it difficult for the prey to detect approaching predators (Schooley et al., 1996). For example, large African herbivores preferentially use open habitats to reduce their chance of being stalked by lions (Valeix et al., 2009). Similarly, open habitats decrease predation risk for a small ground squirrel *Spermophilus townsendii* by increasing the distance at which they can detect predators while also increasing attainable running speeds (Schooley et al., 1996). The relationship between predation risk and cover is therefore not consistent across predator–prey pairs.

When predator detects prey or vice versa, their relative performance capabilities can be critical for determining the outcome of the interaction (Carrascal & Polo, 1999; Elliott et al., 1977; Huey & Hertz, 1984; Husak, 2006a, 2006b; Webb, 1976; Wilson et al., 2018). However, few prey animals flee immediately upon detecting a predator, and may instead employ other anti-predator tactics such as freezing or predator inspection (Caro et al., 2004; Gerkema & Verhulst, 1990). Many animals will not flee until a predator comes within some flight initiation distance to optimise fitness by balancing the costs of and benefits of fleeing (Cooper & Frederick, 2007; Ydenberg & Dill, 1986). Similarly, not all predators immediately engage in an athletic pursuit upon detecting a potential prey, and many use ambush predation either as complete strategy or to get close enough to have a chance of capturing the prey during a high-speed pursuit (Caro, 1994; Harland & Jackson, 2001). If athleticism is required, individuals that can reach faster speeds over shorter time periods (i.e. faster acceleration) often have improved survival (Huey & Hertz, 1984; Husak, 2006a; López & Martin, 2002). Animals can also

use abrupt changes in direction, or manoeuvrability gambits, to outmanoeuvre faster predators (Brown & Taylor, 1995; Howland, 1974; Humphries & Driver, 1970; Wilson et al., 2018). Although speed, acceleration and agility are all important for escaping predators, performing at maximal capacity across all traits is impossible due to biomechanical constraints; the faster an animal runs, the greater its inertia and the harder it is to rapidly change direction and remain stable (Wheatley et al., 2018; Wynn et al., 2015). Thus, animals must trade sprint speed for agility—the faster an animal runs, the lower its agility (Howland, 1974; Wilson et al., 2018).

Once a prey animal is detected, it may be able to mitigate the speed–agility trade-off by making use of obstacles within the habitat. Prey can use obstacles within the habitat, such as trees, shrubs, or rocks, to force a pursuing predator to follow a specific pursuit path (Kruuk & Turner, 1967; Wilson et al., 2015). In open habitats, prey must time the initiation of turning gambits carefully; allowing the predator to move in too close could result in capture, but turning when far away might allow the predator to cut the corner and use a shorter pursuit path (Howland, 1974). Running around obstacles such as trees or shrubs would prevent the predator from cutting corners off the prey's manoeuvrability gambits and might force a closely pursuing predator to slow down to avoid a collision. In fact, both dik-dik *Rhynchotragus kirkii* and oribi *Ourebia ourebi* use fast turns around trees and shrubs to thwart pursuing cheetah *Acinonyx jubatus* (Kruuk & Turner, 1967). Thus, complex habitats might have lower predation risk if the prey is smaller and more agile than its predators, but the agility benefit for these prey will diminish with decreased complexity. Cleared or otherwise simplified habitats may reduce the degree to which the prey can constrain a predator's pursuit path, giving faster predators a performance advantage. This idea is supported in the literature; loss or degradation of habitat can lead to increased predation pressure on small animals (Doherty et al., 2015; McGregor et al., 2015; Pardon et al., 2003). Habitat features can also affect performance capacities directly, as movement can be impeded in features like deep or recently fallen snow or uneven terrain (e.g. Druelle et al., 2019; Murray & Boutin, 1991; Richard et al., 2014). Performance capacities are therefore likely to interact with habitat features in how they affect prey survival.

To determine how particular habitat features affect both the probability of detection by a predator and the chance of escape if detection occurs, we constructed an individual-based model to simulate terrestrial predator pursuits among predators and prey with potentially different biomechanical characteristics. The model allowed us to vary features within the simulated habitat by manipulating the density of obstacles and refuges. We were also able to independently manipulate both the predator and prey's maximum sprint speed, acceleration, deceleration and agility via scaling relationships with limb length (Wilson et al., 2020), which allowed us to explore complex interactions between performance, obstacles and refuges. We predicted that more obstacles would decrease the prey's chance of detection by the predator, giving the prey more opportunities to reach safety and therefore increasing its probability of escape. We also predicted that fast animals with poor agility would

have more difficulty navigating habitats with many obstacles than those with few, and that availability of refuges would be beneficial for prey survival. Consequently, we predicted that prey would have greater survival against faster but less agile predators in complex habitats. Understanding how specific habitat features affect predation for different predator–prey pairs will help us understand these species interactions and assist with identifying combinations of features that should be protected or restored to help conserve vulnerable species.

## 2 | MATERIALS AND METHODS

### 2.1 | Model overview

To simulate a terrestrial predation event, we built an individual-based model using NetLogo v6.1 (Wilensky, 1999). Individual- or agent-based models simulate autonomous individuals interacting with each other and their environment and are an increasingly popular ecological tool (Railsback & Grimm, 2019) as they provide an ideal framework for examining game theoretic interactions among individuals and their environment.

Our model contains mobile predators and prey that interact with each other and with the stationary patches that make up their environment (i.e. refuges, obstacles, target patches and neutral patches).

Various parameters control how the interaction unfolds over time (Table 1). The predator and prey's limb lengths (LL) dictate: their maximum running velocity, their agility (defined as the maximum speed they can turn a radius of 1 m) and their maximum acceleration and deceleration as defined by the scaling relationships in Wilson et al. (2020; described in detail in Appendix S1). We modelled interactions between predators, prey and their habitat in a square with sides of 75 patches (37.5 m using our simulated patch dimensions), where the sides 'wrap' to form a torus which eliminates edge effects. The size of the modelled habitat can be easily adjusted to suit the system in question.

Iterations of the simulation model advance in 0.1 s time steps, with a time limit of 15 simulated minutes. A schematic overview of the model's process is provided in Figure 1. We provide a brief overview of the model processes below, but a detailed description (the ODD specification as per Grimm & Railsback, 2005 and Grimm et al., 2006) of the model is provided in Appendix S2.

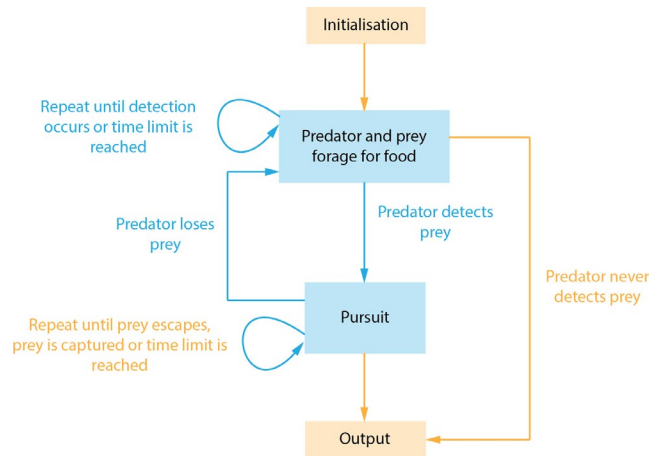
#### 2.1.1 | Detection

After initialisation, the predator and the prey forage throughout the simulated habitat, moving at 30% of their maximum speed in a correlated random walk until they encounter one another. Both can potentially detect other animals within a sector spreading out from

**TABLE 1** Overview of parameters, parameter abbreviations, default values, value ranges and the increments of value changes in the predator–prey model

Parameters	Abbreviation	Default	Range	Increment
Global				
Proportion of obstacles in the habitat	PO	0.05	0–0.2	0.05
Average obstacle radius (m)	OR	1	0.5–2	0.5
Number of refuges	NR	1	0–5	1
Number of target patches	TP	0	0–5	1
Prey and predator				
Limb length (m)	LL	0.5	0.1–1	0.1
Vision distance (m)	VD	15	5–30	5
Vision angle (°)	VA	180	30–330	30
Distance to exhaustion during pursuit (m)	ED	510	10–1010	100
Sensitivity to obstacles	OS	0.99	0.11–0.99	0.44
Prey only				
Freeze distance (m)	FD	10	5–30	5
Flight initiation distance (m)	FID	5	5–30	5
Time between turning gambits (s)	TT	3	1–5	1
Time spent circling an obstacle during pursuit (s)	TC	1	1–5	1
Predator only				
Kill distance (m)	KD	1	0.5–5	0.5

*Note:* Dimensionless parameters are numbers. Unless otherwise specified, default parameter values are used in simulations.



**FIGURE 1** Schematic overview of a terrestrial predator-prey interaction and the processes that cause transitions between behavioural states. Initialisation and output threads are yellow/light, while repetitive internal threads are blue/dark

their forward orientation, comprised of an angle (VA) and a distance (VD). However, the probability of detecting an animal within this sector is influenced by the detector and detectee's relative movement speeds. Moving slowly increases the probability of detecting an animal within the field of view, as it gives the detector more time to search carefully, though this also means the detector covers ground more slowly. We have defined the probability of detection based on the relationship proposed by Gendron and Staddon (1983):

$$P_{\text{detect}} = \left[ 1 - \left( \frac{S}{M} \right)^k \right]^{\frac{1}{k}}, \quad (1)$$

where  $S$  is the detector's current search rate,  $M$  is the detector's maximum possible search rate and  $k$  is the detectee's conspicuousness. We assume the detector can search the width of its vision field every second, so the detector's current search rate is:

$$S = 2\nu \text{VD} \sin \frac{\text{VA}}{2}, \quad (2)$$

where  $\nu$  is the detector's current velocity. We also expect the conspicuousness of the detectee to depend upon its movement speed, as movement often increases the visual and audio cues available to other animals (Caro et al., 2004; Rice, 1983). This may be why many animals employ 'freezing' as an anti-predator response and why some predators exhibit 'cryptic stalking' and freeze when faced by the intended prey (Caro, 1994; Caro et al., 2004; Gerkema & Verhulst, 1990; Harland & Jackson, 2001). Therefore, conspicuousness ( $k$ ) increases with movement speed:

$$k = Re^{H\nu}, \quad (3)$$

where  $R$  and  $H$  are constants that determine how steeply  $k$  increases with the detectee's movement speed,  $\nu$ .

If an animal falls within the predator or prey's field of vision, its probability of detection is calculated as per Equation 1. If the animal

falls within the predator or prey's VD but outside of VA, there is still a small probability of detection by non-visual means, given by:

$$P_{\text{detect}} = \frac{\alpha - 0.5\text{VA}}{180 - 0.5\text{VA}}, \quad (4)$$

where  $\alpha$  is the angular distance between the detector and the detectee.

If the probability of detection is greater than zero, a random float bounded between zero and one is generated, and the animal is 'detected' if this float is less than or equal to the probability of detection.

### 2.1.2 | Pursuit

When the predator detects the prey, it sets an ideal heading,  $h_{\text{ideal}}$ , directly towards the prey. The predator stalks towards the prey at 10% of its maximum velocity until detected, whereupon it accelerates towards maximum velocity. While this is not a strategy employed by all predators (e.g. Ghose et al., 2006; Kane & Zamani, 2014), it is the simplest and therefore easiest to implement, though it can be modified if desired to suit the study species in question. During pursuit, if the prey leaves the predator's field of vision, the predator has a 50% probability of ceasing pursuit and returning to searching (simulating a true 'loss' of the prey). In the other 50% of cases, we assume the predator can interpolate the location of the prey (by non-visual means) and continues to pursue towards it. The prey continues its escaping behaviour in either case.

Upon detecting a predator, the prey's behaviour depends on its distance from the predator. If the detected predator is within the prey's freeze distance (FD) but not within its flight initiation distance (FID), the prey will stop moving. If the detected predator enters the prey's FID, the prey selects an ideal escape heading,  $h_{\text{ideal}}$ , in the opposite direction to the location of the predator and flees, accelerating towards maximum velocity. However, when the prey is headed away from the predator, the predator leaves its detection field; so, after its initial sighting, the prey does not have information on the predator's position relative to its own. To compensate, the prey keeps track of how long it has been since the predator was last 'seen'. A user-defined time after the prey last saw the predator (TT), the prey will make a turning gambit. The purpose of the turning gambit is to alter its heading sufficiently to force the predator to slow down to follow it. However, the prey should never make a turn so great that it ends up running back towards the predator; thus, its turning angle is constrained between 45 and 135° in either direction from its current heading.

### 2.1.3 | Interacting with habitat features

While both the predator and prey have an ideal heading,  $h_{\text{ideal}}$ , their movement in this direction is constrained by features of the habitat and their own performance limitations. The habitat contains a

user-defined number of refuges (NR), target patches (TP) and proportion of obstacles (PO). Escaping prey are drawn towards refuges and target patches, while both predators and prey must avoid obstacles across their behavioural states. We assume prey have prior knowledge of the location of all refuges and target patches within the habitat.

Target patches are patches within the habitat that may be desirable for the prey to run through when escaping, and their location is based on the relative agility of the predator and the prey. If the prey is more agile than the predator, target patches are ones closest to multiple obstacles, usually placed in narrow gaps between obstacles. The agile prey would be able to navigate a path between obstacles easily, where the less agile predator might struggle and have to slow down significantly. Thus, these are places where the prey has a good chance of 'losing' the predator, and they are therefore desirable locations for the prey. Conversely, if the prey is less agile than the predator, target patches are ones furthest from as many obstacles as possible, in clear open spaces. At any point in time, an escaping prey has a desired position,  $p_{\text{desired}}$ , which is set to one of the target patches or a random non-obstacle patch if no target patches have been set. The prey selects a new  $p_{\text{desired}}$  once it arrives at that patch (or has been attempting to reach the patch for more than 60 simulated seconds), to one of the other target patches or to a different random non-obstacle patch within the habitat if no other target patches have been set. The pursuing predator's  $p_{\text{desired}}$  is always the prey's current location. Foraging predators and prey have randomly generated  $h_{\text{ideal}}$  and  $p_{\text{desired}}$ .

Obstacles are patches within the habitat that both the predator and the prey must avoid. They cannot be passed through, and instead must be navigated around. Similar to how refuges have an attractive force towards an escaping prey, obstacles have a repulsive force towards both the predator and the prey, both while foraging and during a pursuit. The strength of this repulsive force is determined by the predator and the prey's obstacle sensitivities (OS). These OS values are bounded between 0 and 1; the larger they become, the more repulsive obstacles are and the more the animals avoid them. An OS of zero means the animal is not repulsed by the obstacles at all, and simply crashes into them. If an escaping prey does collide with an obstacle, it will circle the perimeter for a mean time specified by the user (TC) in an attempt to lose the predator. Obstacles do not occlude the predator or prey's vision and do not influence the probability of detection.

The predator and prey's  $h_{\text{ideal}}$  do not account for the location of obstacles, refuges and target patches. To enable movement that accounts for these factors, a desired heading,  $h_{\text{desired}}$ , is calculated based on the x and y vectors of  $p_{\text{desired}}$ ,  $h_{\text{ideal}}$  and the attractive and repulsive forces the animal experiences from refuges and obstacles.

To calculate the magnitude of the attractive forces acting on an escaping prey at any given position, the attractive force is calculated for the closest refuge:

$$A_x = 500 \frac{1}{d^2} \sin \theta, \quad (5)$$

where  $A_x$  is the x component of the total attractive force acting on the prey,  $d$  is the prey's distance from the refuge and  $\theta$  is the

prey's angle from the refuge. The calculation for the y component of the total attractive force uses  $\cos \theta$  instead of  $\sin \theta$ . Note that the force gets weaker the further away the prey is from the refuge. These forces are set to zero for the predator and foraging prey.

To calculate the magnitude of the repulsive forces acting on the predator or prey at any given position, the repulsive force is calculated for each obstacle, summed and then multiplied by a constant defined by the animal's OS:

$$R_x = \frac{OS}{1 - OS} \times \sum \left( \frac{1}{d^4} \sin \theta \right), \quad (6)$$

where  $R_x$  is the x component of the total repulsive force acting on the prey,  $d$  is the prey's distance from the obstacle and  $\theta$  is the prey's angle from the obstacle.

The x and y vectors of  $p_{\text{desired}}$ ,  $h_{\text{ideal}}$  and the attractive and repulsive forces from refuges and obstacles are then summed together. We then calculate  $h_{\text{desired}}$  by taking  $\tan^{-1}$  of the resultant x and y coordinates. The animal will attempt to turn towards  $h_{\text{desired}}$ , but it is constrained by its agility at its current speed. If the angle of the desired turn is too great, it will make as large a turn as possible towards its  $h_{\text{desired}}$ , and simultaneously decelerate as much as it can over that time period.

## 2.1.4 | Output

A simulation runs until one of the following conditions is met: (a) the prey enters a refuge, (b) the predator reaches its exhaustion distance, ED, (c) the prey is captured or (d) the simulation's time limit is reached. Under conditions a, b and d, the prey is considered to have escaped. The predator captures the prey if it comes within a pre-defined kill distance (KD).

At the completion of each interaction, the model records whether the prey was detected by the predator and whether the prey escaped (as binary variables), the time it took for the prey to be detected by a predator (s), the duration of the prey's escape (s) and the duration of the simulation (s). It also records the lengths of the prey's escape path (m) and the predator's pursuit path (not including distance while stalking; m).

## 2.2 | Sensitivity analysis

To analyse the first-order (single parameter) and second-order (two-way parameter interaction) effects on the model output, we used a reduced factorial design where each parameter was varied across its range with every other parameter in pairs (a total of 8,558 parameter combinations; see Table 1 for parameter default settings and ranges). We ran 100 simulation replications per parameter combination, resulting in 855,800 simulations. For each parameter combination, the mean of the prey's escapes and

captures when the prey avoided detection, was detected, and overall, along with the median detection time, escape time, prey's escape path length and predator's pursuit path length if a detection occurred were calculated. The summarised output variables were transformed to fit a normal distribution; the probabilities of a prey escaping under the different conditions were arcsine square root transformed, and the median detect time, median pursuit time, median prey escape path length and median predator pursuit path length were all square root transformed. The appropriately transformed, summarised outputs were then analysed using the MULTISENSI v.2.1.1 (Lamboni et al., 2009, 2011) package in R v.4.0.0. First-order sensitivity indices describe the weighted effect of a single parameter on each model response when all other parameters were held constant, while second-order sensitivity indices describe the weighted effect of each parameter when two parameters were allowed to vary simultaneously. Generalised sensitivity indices calculated using MANOVA decomposition of inertia (Lamboni et al., 2011) were also generated, which give an overall weight to each parameter across all model responses.

### 2.3 | Effect of relative performance, obstacles and refuges on detection and escape

To investigate the two-way effects of performance, obstacles and refuges on the prey's chance of avoiding detection and/or of escaping, 500 additional simulations were performed for a hypothetical predator and prey, where predator and prey's relative limb length varied with the proportion of obstacles (PO, 0–0.2) and number of refuges (NR, 0–5) in the habitat. The prey had LL = 0.5 m, FD = 15 m, FID = 10 m, VA = 240°, TC = 3 s and ED = 1,000 m. The predator had VD = 20 m, ED = 1,000 m and LL was varied from 0.1 to 1.0 m. The mean obstacle radius (OR) was set to 1.5 m. All other parameters used default settings (Table 1).

### 2.4 | Case study: Cheetah and impala in open savanna and acacia thicket

To determine whether our model predictions represent real ecological outcomes, we parameterised and ran the model for a cheetah *A. jubatus* preying on an impala *Aepyceros melampus* in two different habitats: open savanna and acacia thicket. Mills et al. (2004) estimated that cheetah have a kill rate of 23% (equivalent to a 77% prey escape rate) in open savanna habitat, compared to 11% (89% escape rate) in acacia thicket.

As both cheetah and impala are large animals with fast movement speeds, the habitat size was increased to 200 × 200 patches (equivalent to 100 m × 100 m). Because impala cannot utilise refuges in either of these habitats and because we lacked information regarding the use of target patches, both NR and TP were set to 0 (Table 2). The PO in each habitat was estimated from photographs (Gertenbach, 1983) and set to 0.01 for open savanna, and

**TABLE 2** Parameter settings for cheetah versus impala case study

Parameter	Value	Reference
<b>Global</b>		
Proportion of obstacles in the habitat	0.01 (open savanna), 0.1 (acacia thicket)	Gertenbach (1983) Gertenbach (1983)
Average obstacle radius (m)	1.5	
Number of refuges	0	
Number of target patches	0	
<b>Impala</b>		
Maximum velocity (m/s)	13.8	Wilson et al. (2018)
Agility (m/s)	3.429	Wilson et al. (2018)
Acceleration (m/s <sup>2</sup> )	5.7	Wilson et al. (2018)
Deceleration (m/s <sup>2</sup> )	−6.3	Wilson et al. (2018)
Vision distance (m)	50	
Vision angle (°)	240	
Freeze distance (m)	50	
Flight initiation distance (m)	30	for <i>Eudorcas thomsonii</i> (Kruuk & Turner, 1967; Schaller, 1968)
Exhaustion distance (m)	800	
Time between turning gambits (s)	3	
Time spent circling an obstacle during pursuit (s)	3	
Obstacle sensitivity	0.99	
<b>Cheetah</b>		
Maximum velocity (m/s)	19.9	Wilson et al. (2018)
Agility (m/s)	3.569	Wilson et al. (2018)
Acceleration (m/s <sup>2</sup> )	8.3	Wilson et al. (2018)
Deceleration (m/s <sup>2</sup> )	−10.6	Wilson et al. (2018)
Vision distance (m)	50	
Vision angle (°)	180	
Exhaustion distance (m)	300	Schaller (1968) and Wilson et al. (2013)
Kill distance (m)	0.66	Wilson et al. (2018)
Obstacle sensitivity	0.99	

0.1 for acacia thicket, while OR was set to 1.5 m in both habitats (Table 2).

Cheetah and impala performance capabilities were estimated directly from Wilson et al. (2018; Table 2). The cheetah and impala's VD were both set to 50 m to ensure they could not see the entirety of the simulated habitat at once, and VA was set to 180° for the cheetah and 240° for the impala (Table 2). The impala's ED was set to 800 m (500 m longer than the cheetah's), as cheetahs engage in short, high-speed pursuits rather than endurance hunting (Wilson et al., 2013) and are therefore likely to exhaust before their prey.



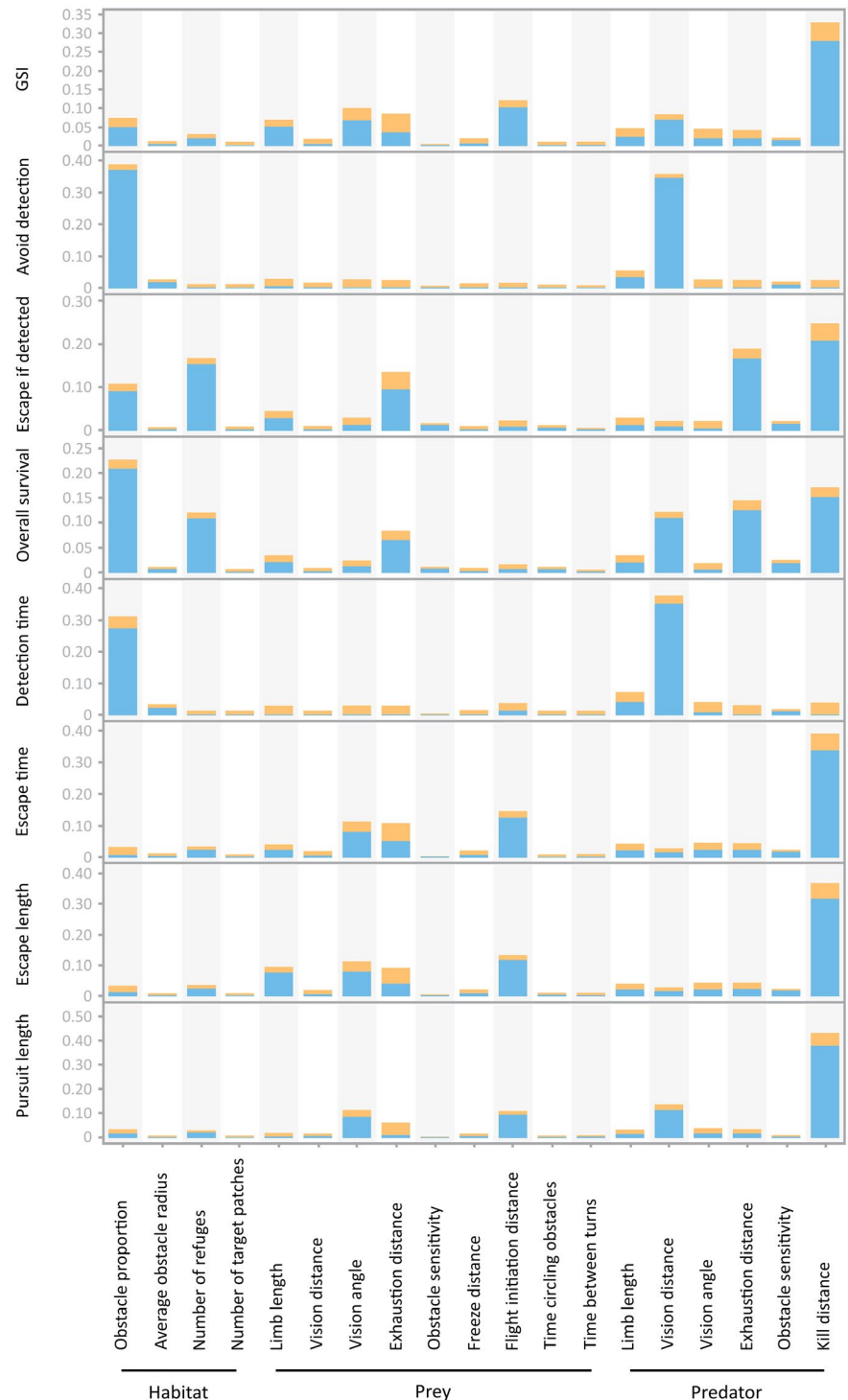
TT and TC were set to 3 s each, as we would expect the impala to make use of frequent turning and athleticism to compensate for the cheetah's much faster maximum velocity (Wilson et al., 2018; Table 2).

We ran 500 simulations per habitat to generate estimates for the impala's probability of escaping if detected. The resulting estimates were analysed using a two-sample test for equality of proportions using the *prop.test* function in R v.4.0.0.

### 3 | RESULTS

#### 3.1 | Sensitivity analysis

When all other parameters were held constant, the kill distance (KD) had the greatest first-order effect across all model responses (based on the generalised sensitivity index), followed by the prey's flight initiation distance (FID), the predator's vision distance (VD)



**FIGURE 2** First- and second-order sensitivity indices for each parameter's effect on each model response. First-order indices (blue/dark) indicate the parameters' effects when all other parameter values are held constant; second-order indices (yellow/light) indicate the parameters' main effects in addition to their two-way interactive effects with all other parameters. Generalised sensitivity indices (GSI) describe each parameter's effect across all model responses

and the prey's vision angle (VA; Figure 2). When two parameters were permitted to vary at once, the parameters with the highest second-order effects were KD, FID, the prey's VA and the prey's exhaustion distance (ED; Figure 2).

Broken down into individual model responses, the four parameters with the largest first-order effects on the prey's chance of avoiding detection were the proportion of obstacles in the habitat (PO), the

predator's VD, the predator's limb length (LL) and the average obstacle radius (OR; Figure 2; Table 3). The proportion of obstacles, predator's VD, predator's LL and the prey's LL had the largest second-order effects on the prey's chance of avoiding detection (Figure 2).

The prey's chance of escaping if detected was most affected by the first-order effects of the KD, the predator's ED, the number of refuges (NR) and prey's ED (Figure 2; Table 3). These four parameters

Model response	With default settings	With min. setting	With max. setting
Probability of avoiding detection (%)	2.42		
Proportion obstacles		0.33	35.61
Predator's vision distance		45.22	0.00
Predator's limb length		2.94	6.67
Average obstacle radius		7.67	1.28
Probability of escaping if detected (%)	17.19		
Kill distance		22.36	0.68
Predator's exhaustion distance		66.25	15.22
Number of refuges		2.33	42.06
Prey's exhaustion distance		1.08	22.45
Overall probability of survival (%)	19.19		
Proportion obstacles		17.11	65.78
Kill distance		24.17	3.22
Predator's exhaustion distance		66.94	18.00
Predator's vision distance		57.61	14.83
Median time to detection (s)	144.50		
Predator's vision distance		342.03	44.35
Proportion obstacles		106.18	350.60
Predator's limb length		156.55	196.15
Average obstacle radius		202.70	126.70
Median escape time (s)	51.25		
Kill distance		103.13	0.00
Flight initiation distance		51.25	99.35
Prey's vision angle		1.55	63.85
Prey's exhaustion distance		2.35	55.05
Median prey escape path length (m)	132.47		
Kill distance		264.20	0.00
Flight initiation distance		132.47	257.43
Prey's vision angle		2.15	159.75
Prey's limb length		145.24	47.54
Median predator pursuit path length (m)	15.93		
Kill distance		27.99	0.00
Predator's vision distance		3.29	30.65
Flight initiation distance		15.93	27.16
Prey's vision angle		2.54	23.74

**TABLE 3** Variation in model responses with default, minimum, and maximum settings for the four parameters with the largest first-order sensitivity indices

Note: Probability of escaping if detected, median time to detection, median prey escape time, median prey escape length and median predator pursuit length (not including time spent stalking) are all conditional upon the prey being detected by the predator.



also had the largest second-order effects on the prey's chance of escaping if detected (Figure 2).

The four parameters with the greatest effects on the prey's overall chance of survival were PO, KD and the predator's ED and VD (Figure 2; Table 3). These four parameters also had the largest second-order effects on the prey's overall chance of survival (Figure 2).

The median time to detection was most influenced by the predator were the predator's VD, PO, the predator's LL and OR (Figure 2; Table 3). The predator's VD, PO and the predator's LL and VA had the largest second-order effects on median detection time (Figure 2).

The four parameters with the largest first-order effects on median escape time were the KD and the prey's FID, VA and ED (Figure 2; Table 3). These four parameters also had the largest second-order effects on the median escape time (Figure 2).

The median escape path length for the prey was most influenced by the KD and the prey's FID, VA and LL (Figure 2; Table 3). These four parameters also had the largest second-order effects on the median escape path length (Figure 2).

Finally, the four parameters with the largest first-order effects on the median predator pursuit path length were the KD, the predator's VD and the prey's FID and VA (Figure 2; Table 3). These four parameters also had the largest second-order effects on median pursuit path length.

Full tables of first- and second-order sensitivity indices are presented in Appendix S3.

## 3.2 | Effect of relative performance, obstacles and refuges on detection and escape

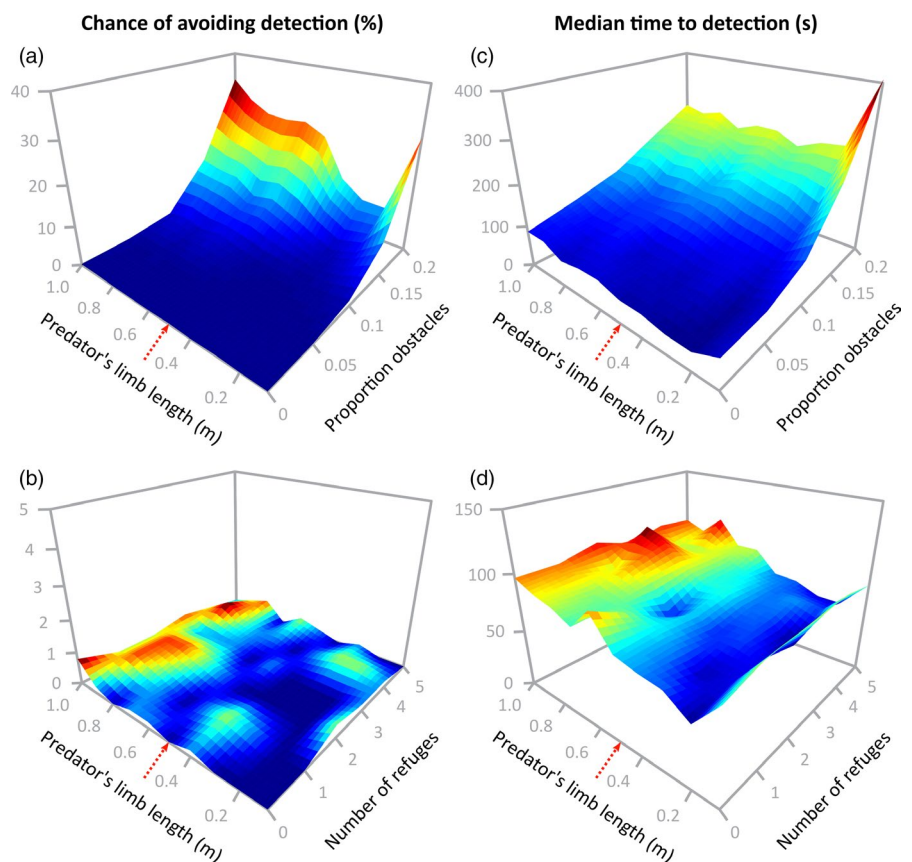
### 3.2.1 | Chance of avoiding detection

The prey was most likely to avoid detection by the predator when there was a high proportion of obstacles in the habitat (Figure 3a). A high proportion of obstacles reduced the prey's chance of detection the most when the predator was either much faster but less agile or much slower and more agile than the prey (Figure 3a). The number of refuges had little effect on the prey's chance of avoiding detection (Figure 3b).

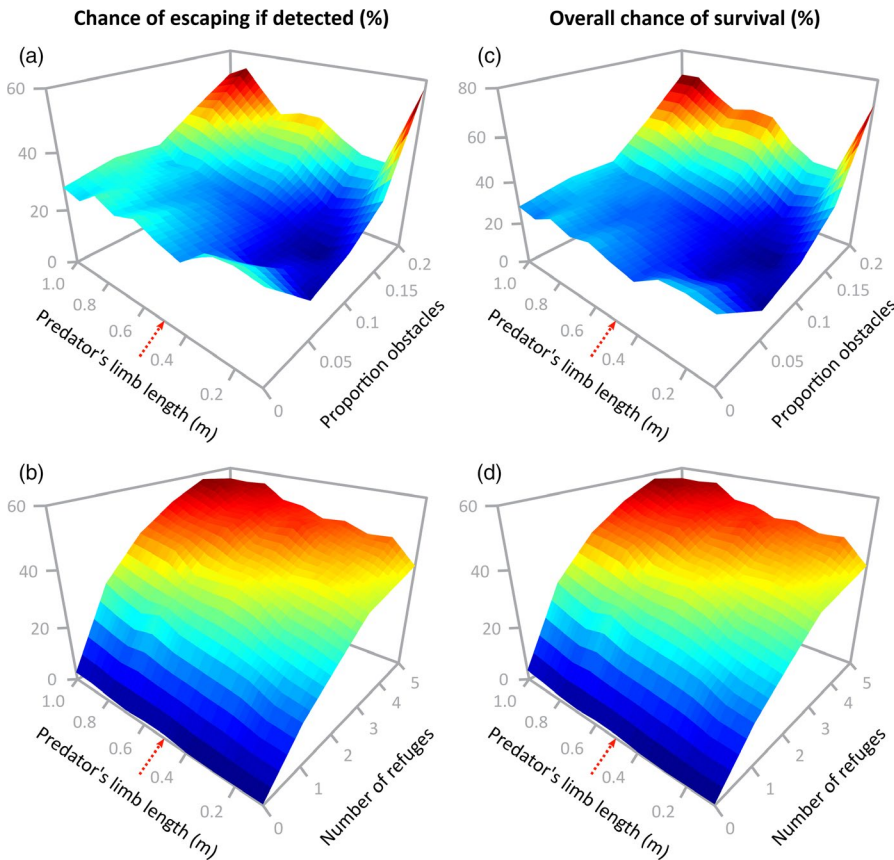
If the prey was detected, the median time to detection was longer in habitats containing many obstacles than few and this relationship was strongest when the predator was slower and more agile than the prey (Figure 3c). The number of refuges had no discernible effect on the median time to detection (Figure 3d).

### 3.2.2 | Chance of escaping if detected

If detected, the prey was more likely to escape when more obstacles were present in the habitat (Figure 4a). This effect was most dramatic when the predator was either much faster and less agile than the prey, or much slower and more agile than the prey (Figure 4a). However, when the predator had similar performance capabilities to the prey, the proportion of obstacles had the least effect on the chance of escape (Figure 4a).



**FIGURE 3** Interaction between relative performance (controlled via relative limb length) and habitat features on the prey's chance of avoiding detection (a, b) and, if detected, the median time to detection (c, d). The prey's limb length was held constant at 0.5 m (indicated by the red dashed arrow). For (a) and (c), number of refuges was held constant at 1; for (b) and (d), proportion obstacles was held constant at 0.05



**FIGURE 4** Interaction between relative performance (controlled via relative limb length) and habitat features on the prey's chance of escaping if detected (a, b) and the prey's overall chance of survival (c, d). The prey's limb length was held constant at 0.5 m (indicated by the red dashed arrow). For (a) and (c), number of refuges was held constant at 1; for (b) and (d), proportion obstacles was held constant at 0.05

The prey's chance of escape increased dramatically in the presence of a refuge (from approximately 0%–60%; Figure 4b). The presence of additional refuges continued to increase the prey's chance of escape, but this increase started to plateau at roughly three refuges (Figure 4b). Additional refuges increased the prey's chance of escape slightly more rapidly from faster, less agile predators than from slower but more agile predators (Figure 4b).

### 3.2.3 | Overall chance of survival

When the probability of avoiding detection and the probability of escaping if detected were combined, the prey was most likely to survive in the most complex habitats containing 20% obstacles, irrespective of the predator's relative performance (Figure 4c). However, the shape of the relationship between the proportion of obstacles in the habitat and the prey's overall chance of survival varied depending on the predator's relative performance (Figure 4c).

The prey was more likely to survive all sizes of predator when there were more refuges available (Figure 4d).

### 3.3 | Case study: Cheetah and impala in open savanna and acacia thicket

The impala's chance of escaping if detected by the cheetah was significantly higher in acacia thicket ( $23.15 \pm 4.59\%$ ,  $n = 324$ )

than open savanna ( $13.92 \pm 3.27\%$ ,  $n = 431$ ;  $\chi^2 = 10.724$ ,  $df = 1$ ,  $p = 0.001$ ).

## 4 | DISCUSSION

Our model provides a theoretical framework for understanding how obstacles and refuges affect predation risk for specific predator and prey pairs in high-speed terrestrial pursuits. The model's estimates for impala escape success were much lower than those observed in reality (23% vs. 89% in open savanna and 14% vs. 77% in acacia thicket), but the difference in escape success between habitats was relatively accurate (9% vs. 12%). Because our model assumes the predator captures the prey as soon as it comes within the killing distance, we would expect escape success to be consistently underestimated. Real prey typically resist capture, sometimes fighting the attacking predator, and are often successful in escaping (Lingle & Pellis, 2002). With this limitation in mind, our model successfully predicts the relative success of impala escaping cheetah in open savanna and acacia thickets with reasonable accuracy.

In our general experiments, prey had the best chance of avoiding detection by a predator in habitats containing an abundance of obstacles and this relationship was strongest when the predator was faster but less agile or slower and more agile than the prey. Conversely, the relationship was weakest when the predator was just slightly slower and more agile than the prey. Because obstacles constrain movement speeds, both the predator and prey are forced to forage more slowly

through complex habitats than open ones. Consequently, both predator and prey will cover ground more slowly when there are many obstacles and are therefore less likely to encounter one another during a simulation of limited duration. This effect was most apparent when the predator was either much less agile or very slow relative to the prey. Both scenarios could result in the predator moving more slowly through the habitat than the prey; either because the predator has such poor agility that it must slow down substantially to make the required manoeuvres or because it is intrinsically slow all the time. If the prey was detected, the median time to detection was longest in the presence of many obstacles, especially when the predator was very slow relative to the prey. Refuges had little effect on the prey's probability of avoiding detection.

If detected, the prey had the best chance of escaping a faster but less agile predator in complex habitats with a high abundance of obstacles, and the lowest chance of escape in simple habitats with few obstacles. This effect was even more dramatic when the predator was very slow but very agile compared to the prey. This suggests that obstacles may affect the prey's chance of escape in more than one way. First, our prediction that obstacles affect prey survival via their interaction with the speed-agility trade-off generally appears to hold. When there are no obstacles to slow down a faster predator and constrain its pursuit path, a slower prey should have a poorer chance of survival than when many obstacles are present, which our results demonstrate. However, we also found the prey had an equally high chance of escaping a much slower but more agile predator in a habitat containing many obstacles as it did in one with no obstacles. Because the prey determines its escape path during a pursuit while the predator follows, the prey can make split second decisions about where to move (e.g. to swerve and thus avoid an obstacle) while the predator must constantly respond to the prey's manoeuvres. A pursuit predator is therefore more likely to collide with an obstacle when moving at high speeds in a complex habitat, even if it is relatively agile. This might explain why pursuit predators will sometimes use alternative hunting strategies in complex habitats (Eaton, 1970; Schaller, 1968). For example, cheetahs hunting in open savanna habitats tend to engage in high-speed pursuits with little to no stalking (Kruuk & Turner, 1967) but behave more like ambush predators when hunting in complex scrub thickets (Eaton, 1970) even though they can often be just as agile as their prey (Wilson et al., 2018). However, our model suggests this theory only appears to hold when the predator is much slower than the prey; in scenarios where the predator is only slightly slower but more agile than the prey, obstacles do not increase the prey's chance of escape anywhere near as much. In contrast to the proportion of obstacles, more refuges increased the prey's chances of escape regardless of the predator's relative performance. This result is intuitive, as a higher abundance of refuges increases the likelihood that one will be nearby when the prey is detected by the predator.

Overall, prey had the highest chance of survival in complex habitats containing an abundance of both obstacles and refuges. These results support our prediction that habitat features have major consequences for prey survival via their interaction with performance

and behaviour. In certain systems, habitat modification is likely to cause increased vulnerability to predators not only because it reduces available shelters but also because larger, faster predators have a performance advantage in open habitats. This finding has important implications both for our understanding of predator-prey interactions and for conservation of threatened species. Numerous species world-wide are threatened by invasive predators (Burbidge & Manly, 2002; Caut et al., 2008; Hooper et al., 2005) and modification of habitat (Brooks et al., 2002; Fahrig, 1997; Pimm & Raven, 2000). Notably, the combination of habitat modification and the presence of feral cats and foxes has caused substantial decreases in Australian critical weight range (35–550 g) mammals (Burbidge & McKenzie, 1989; McKenzie et al., 2007; Newsome, 1975). Our model not only provides possible mechanistic explanations for this phenomenon, but it also forms a valuable tool for determining which habitat features are most likely to increase survival of vulnerable species against these predators and therefore which habitat features should be protected or replaced. Parameterised with the appropriate performance and behavioural data, our model's predictions could be used to prioritise conservation of key habitat features or aid in habitat regeneration efforts.

While our model provides a comprehensive method of assessing the effect of specific habitat features on predation risk in a general setting, it has several limitations. We investigate how obstacles and refuges influence terrestrial predator-prey interactions, but there are a myriad of other landscape features that can affect the behaviour and performance of predators and prey, including snow cover, uneven terrain and surface friction and narrowness (Bergman et al., 2006; Druelle et al., 2019; Wheatley, et al., 2018; Wheatley et al., 2018). For example, snow can reduce maximum achievable velocity while simultaneously increasing the energetic costs of movement (Parker et al., 1984), and morphological adaptations such as foot-loading can determine how well predators and prey fare in such habitat features (Murray & Boutin, 1991). Other limitations involve predator and prey behaviour. For instance, the prey's escape strategy was not dependent on either the size of the pursuing predator or the complexity of the habitat. In reality, many animals adjust their escape strategies based on the identity and/or performance capabilities of the pursuing predator (Bulbert et al., 2015; Eilam, 2005; Fichtel, 2007; Furuichi, 2002; Ilany & Eilam, 2008; Walther, 1969). Similarly, animals will often adopt different anti-predator behaviours and escape responses based on distance to cover, familiarity with the terrain, the predator's proximity and approach speed, how conspicuous the prey feels and in response to social behaviours (Clarke et al., 1993; Cooper, 1997, 1998, 2009; Dill, 1990; Kramer & Bonenfant, 1997; Martin & López, 1995; Quadros et al., 2019). Our model could be modified to investigate different anti-predator, escape or predation strategies based on either biotic or abiotic factors. For instance, the prey's behaviours could be adjusted such that it recognises types of predator and responds accordingly. Similarly, predators could be coded to respond differently to prey in certain habitats, potentially switching to a sit-and-wait tactic in complex habitats as discussed above. The prey could also be coded to detect the distance to the

nearest refuge at the start of a pursuit and either head straight for it or use turning gambits depending on the distance to safety. Future studies could modify our model to these purposes and investigate the effects of habitat on prey survival under such constraints.

Most studies examining the effect of obstacles on performance consider animals climbing or jumping over obstacles rather than moving around them (Kohlsdorf & Biewener, 2006; Krell & Patla, 2002; Pelletier & McLeod, 1994; Sparrow et al., 1996; Tucker & McBrayer, 2012). Moving over obstacles is not always possible; large obstacles may be too high to step over, and many animals are not capable of climbing. We have simulated a scenario where moving over obstacles is impossible for either predator or prey, and they must instead navigate a path around obstacles. Our model demonstrates that obstacles constrain movement speed choices through their interactions with biomechanical trade-offs, such as the one between speed and agility. Certain species are therefore likely to have a performance advantage against less agile predators in complex terrain, leading to reduced vulnerability to predation. In these cases, a reduction or simplification of complex habitat may result in a lower survival for vulnerable species. Future studies should quantify the performance capabilities of vulnerable animals and their major terrestrial predators to test this hypothesis and to consider the interaction between habitat features and performance when undertaking conservation efforts.

## ACKNOWLEDGEMENTS

We wish to acknowledge The University of Queensland's Research Computing Centre (RCC) and the DEEP Research Group (University of Tasmania) for their support in this research. We also thank Simone Blomberg for advice on sensitivity analysis, Gwendolyn David for help with figure construction, and Rory Wilson, four anonymous reviewers and numerous other researchers at conferences for excellent discussion and suggestions for refining the model. This work was funded by an Australian Research Council Discovery grant (DP180103134) to R.S.W. and T.P.P. and a University of Queensland Graduate School International Travel Award to R.W.

## AUTHORS' CONTRIBUTIONS

R.W., T.P.P., O.L. and R.S.W. conceived the ideas and designed the model; R.W. and T.P.P. constructed the model and R.W. ran simulations, analysed results and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

NetLogo code, R code, and data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.wm37pvmkm> (Wheatley et al., 2020).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Wheatley R, Pavlic TP, Levy O, Wilson RS. Habitat features and performance interact to determine the outcomes of terrestrial predator-prey pursuits. *J Anim Ecol*. 2020;00:1–14. <https://doi.org/10.1111/1365-2656.13353>