

# Optimal web investment in sub-optimal foraging conditions

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**Abstract** Orb web spiders sit at the centre of their approximately circular webs when waiting for prey and so face many of the same challenges as central-place foragers. Prey value decreases with distance from the hub as a function of prey escape time. The further from the hub that prey are intercepted, the longer it takes a spider to reach them and the greater chance they have of escaping. Several species of orb web spiders build vertically elongated ladder-like orb webs against tree trunks, rather than circular orb webs in the open. As ladder web spiders invest disproportionately more web area further from the hub, it is expected they will experience reduced prey gain per unit area of web investment compared to spiders that build circular webs. We developed a model to investigate how building webs in the space-limited microhabitat on tree trunks influences the optimal size, shape and net prey gain of arboricolous ladder webs. The model suggests that as horizontal space becomes more limited, optimal web shape becomes more elongated, and optimal web area decreases. This change in web geometry results in decreased net prey gain compared to webs built without space constraints. However, when space is limited, spiders can achieve higher net prey gain compared to building typical circular webs in the same limited space. Our model shows how spiders optimise web investment in sub-optimal conditions and can be used to understand foraging investment

trade-offs in other central-place foragers faced with constrained foraging arenas.

**Keywords** Spider web · Ladder web · Optimal foraging · Central-place foraging

## Introduction

Central-place foraging theory predicts that an animal's foraging arena will be approximately circular when prey are distributed evenly, when time to reach prey is critical and when the animal's speed is the same in all directions (e.g. Horn 1968). For most orb web spiders, the web is indeed circular, or slightly vertically elongated, as gravity allows spiders to run faster down than up (Herberstein and Heiling 1999; Zschokke and Nakata 2010). Notable exceptions are ladder web spiders that build highly elongated orb webs up to seven times taller than wide (e.g. Eberhard 1975). Ladder web spiders, therefore, deviate from predictions of central-place foraging theory. While some ladder web species elongate their webs to specialise on moth prey (*Scoloderus*, Eberhard 1975; Stowe 1978), most are strictly arboricolous (build against tree trunks) and are not prey specialists, but elongate their webs in response to horizontal space constraints for web building (e.g. *Telaprocera*, Harmer 2009; Harmer and Herberstein 2009; *Clitaetra*, Kuntner et al. 2008; Kuntner and Agnarsson 2009; *Cryptaranea atriastula*, Forster and Forster 1985). For *Telaprocera* that build webs against tree trunks (Fig. 1a), web elongation (height/width ratio) is determined by tree diameter, with narrower trees leading to more elongated webs (Harmer 2009).

For ladder web spiders, adding area to the top and bottom of webs when space is limited increases web area

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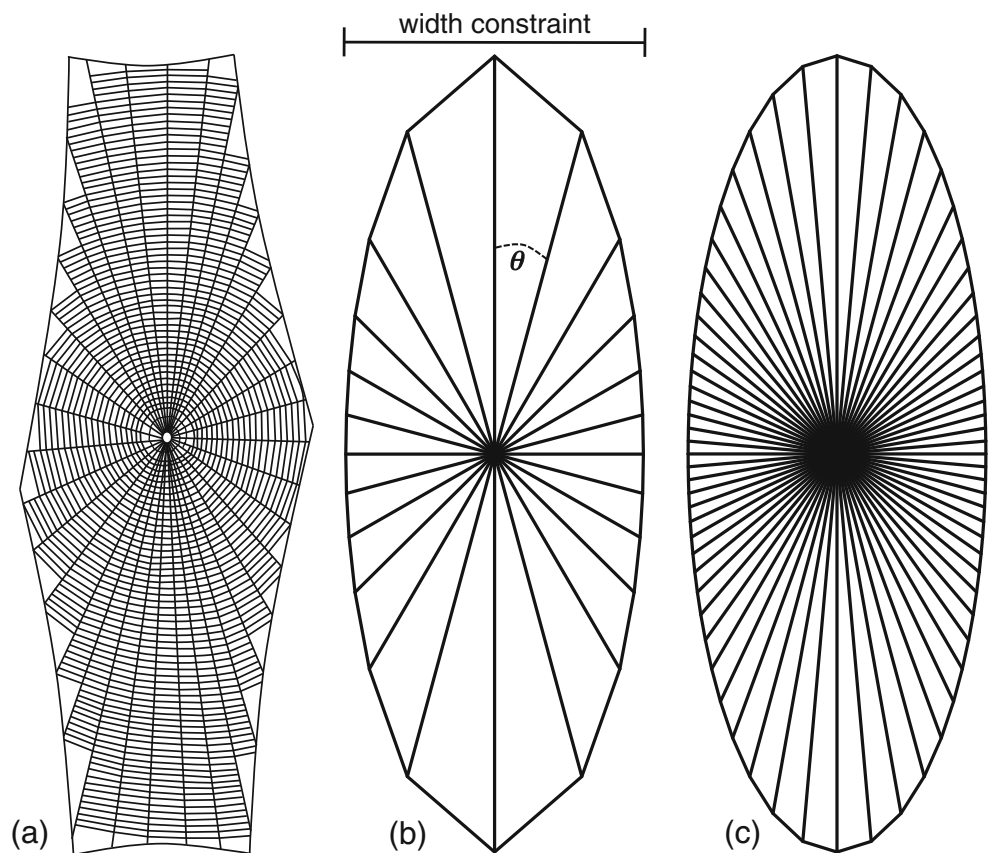
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**Fig. 1** **a** Schematic representation of an arboricolous ladder web of *T. maudae*. The web is usually built about 1–3 cm from the tree surface and anchored to bark projections or across depressions in the trunk.

*Telaprocera* webs run tangential to the tree surface and do not curve around the tree like *Herennia* ladder webs. **b**

Schematic demonstrating how web shape and area were modelled. Webs were modelled as ellipses comprised of triangular wedges emanating from the hub. The number of wedges per web was determined by the angle  $\theta$ . Web width at the hub was constrained while the vertical radius was allowed to increase freely. **c** Decreasing the angle  $\theta$  results in an increased number of triangular wedges per web giving a more accurate approximation of net gain



and thus enhances prey interception. However, webs do not retain prey indefinitely, with many prey escaping within seconds after contacting the web (e.g. Nentwig 1982; Blackledge and Zevenbergen 2006; Zschokke et al. 2006). Because the speed at which a spider can traverse its web is finite, addition of more area further from the web hub will result in diminishing returns. That is, building larger webs does not necessarily result in sufficiently added prey capture relative to building costs, as prey are likely to escape before the spider can reach them.

As the radius of circular webs increases, added area and prey interception potential are distributed evenly in all directions from the spider at the hub (assuming similar up and down running velocities; where asymmetries are larger, we expect a bias towards a larger lower web half). For ladder webs, when web diameter reaches a horizontal constraint, area can only be added to the top and bottom of the web. This means that added area is disproportionately further from the hub compared to a circular web. Consequently, prey intercepted near the top and bottom web edges require longer travel times and have a higher probability of escape. This uneven distribution of foraging investment raises the question of whether arboricolous ladder web spiders are foraging optimally and achieving maximum prey capture for their foraging investment.

Here, we develop a model to understand how horizontal web constraints influence relative net resource gain and the optimal size and shape of arboricolous ladder webs. Assuming that spiders build webs to maximise resource gain under given width constraints, we show that (1) building elongated webs in the space-limited conditions on tree trunks lowers the maximum potential resource gain achievable if no space constraints were present and, (2) nevertheless, when horizontal space is limited, spiders achieve higher relative net resource gain by elongating their webs compared to building circular webs in the same space.

## Materials and methods

A model was developed that assumes spiders build webs for maximal net resource gain (a proxy for fitness). For a simple circular web, net gain  $W$  is equal to prey captured  $N$  minus web building costs  $C$ , which are both a function of web radius  $R$ :

$$W(R) = N(R) - C(R) \quad (1)$$

where web cost  $C(R)$  is proportional to web area:

$$C(R) = c\pi R^2 \quad (2)$$

where  $c$  is an arbitrary constant that reflects cost of web building per unit area of web. Prey captured per unit time  $N(R)$  is proportional to the product of web area and the probability a spider will reach the prey before it escapes:

$$N(R) = n \int_0^R 2\pi r \int_{\frac{c}{v}}^{\infty} f(t) dt dr \quad (3)$$

where  $n$  is an arbitrary constant that reflects overall prey availability,  $v$  is spider velocity and  $f(t)$  is the prey escape time distribution. For a given web cost per unit area  $c$  and prey availability  $n$ , there exists an optimal web radius  $R$  that maximises net gain. The model assumes that spiders rest approximately at the web centre and that prey intercept the web randomly in space. Prey escape times are shown elsewhere to be log-normally distributed, where most prey escape within the first few seconds and fewer prey are retained as time increases (e.g. Blackledge and Zevenbergen 2006).

We extended the circular web model to accommodate elongated ladder webs, which we modelled as ellipses beyond their horizontal constraint, as this simply and accurately captures web shape (Fig. 1a). Webs are widest at the hub and taper towards the top and bottom. They do not possess the parallel sides or vertical perpendicular pseudoradii threads that bypass the hub as in *Heremia* ladder webs (Kuntner 2005). The tapered ends of *Telaprocera* webs likely reflect a constraint in their building behaviour that prevents them from building more parallel-sided webs and hence from building webs that occupy all available space within a given width constraint and optimal vertical radius. Therefore, our model predicts the resource gain differential between observed webs (approximated by an ellipse) and webs built in “ideal” (i.e. unconstrained) conditions, and between observed webs and typical circular orb webs built within the same horizontal constraint. Because the analytical solution was non-trivial, we developed a geometric model to approximate net gain using triangular wedges. Wedges emanated from the web hub by distances that were a function of angle  $\theta$  and approximated the target web dimensions (Fig. 1b). Progressively decreasing the angle at the hub (and subsequently increasing the number of wedges per web) resulted in an increasingly good approximation of net gain (Fig. 1c). The web building cost and added prey per wedge were summed to give whole-web totals. Net gain was calculated for a given horizontal constraint and spider velocity by increasing the size of a web until maximum added prey was reached. While we did not directly measure homogeneity of prey retention times across the web, mesh spacing is very consistent in *Telaprocera* webs (A.M.T. Harmer, personal observation), and so we assumed uniform stickiness with a linear decrease in prey value (as a function of time) from the hub to the web periphery.

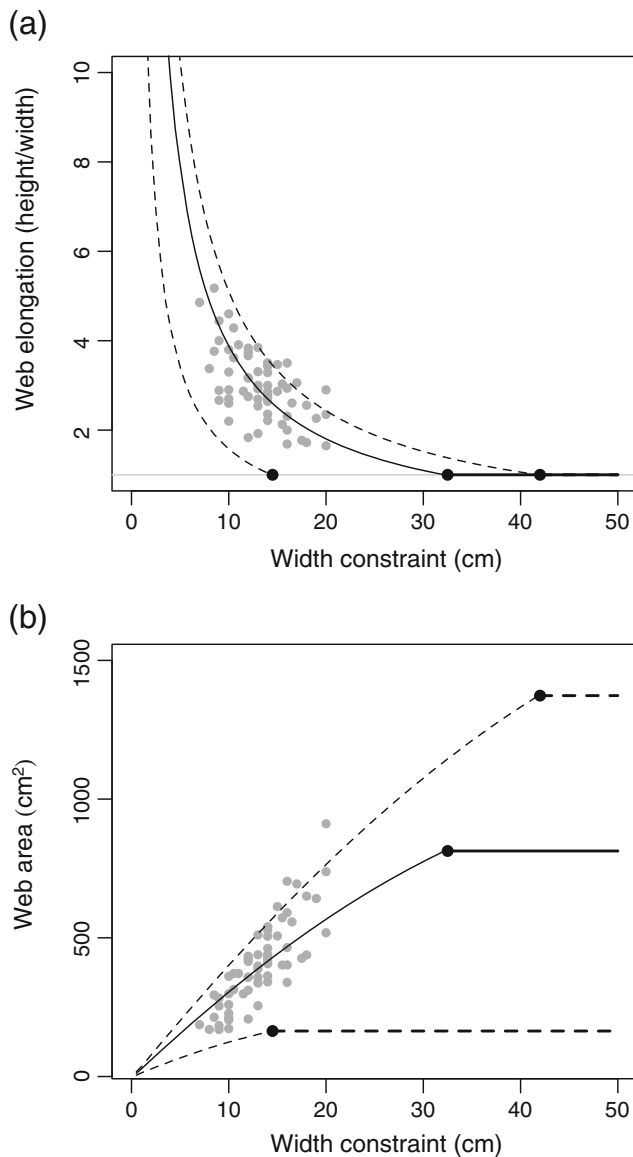
The running velocity  $v$  of *Telaprocera madae* spiders was determined from videos of spiders catching prey in their webs ( $n=6$ , mean=2.31 cm/s, range=1–3 cm/s). We assumed that ladder webs measured in the wild were maximised for net gain, and therefore, we fitted the elliptical web model to field measurements of web elongation (*T. madae*, Harmer 2009) to find the best-fit prey escape distribution. Model fitting was done using the optim function in the software R (R Development Core Team, 2010).

## Results and discussion

The best-fit prey escape distribution suggested a mean prey escape time of 0.32 s and 95% prediction interval of 0.01 to 12.59 s. Allowing the prey escape distribution parameter to vary freely when fitting the model leads to a number of potential curves describing the relationship between width constraints, web area and elongation; a visual inspection suggests that the best-fit values capture the relationship adequately (Fig. 2a, b) and that our model captures the underlying processes determining web elongation. The empirically derived range of spider running velocities adequately captured the variation in web measures from the field (Fig. 2a, b), further indicating that web architectural features are better understood with models incorporating web building decisions, rather than with purely phenomenological methods of fitting lines (or curves) to observed data.

When there are no horizontal space constraints, the optimal web shape for maximum resource gain is circular (compare black circles in Figs 2a and 3). Logically, when there are no width constraints, a circular web is always optimal as all web edges are equidistant from the hub. However, as horizontal space becomes limited, optimal web shape becomes increasingly elongated (Fig. 2a), and optimal area decreases (Fig. 2b). In other words, as horizontal space is constrained, spiders invest some silk vertically beyond the optimal circular radius, which will return some prey, although at a reduced rate compared to areas within the optimal circular radius (the area added vertically beyond the optimal circular radius is less than the area saved by not building beyond the horizontal constraint). This explains why the optimal area decreases as horizontal space becomes more limited.

Increasing web elongation and decreasing web area as horizontal space becomes more limited result in reduced net gain compared to the global maximum (i.e. no width constraints; Fig. 3). For a spider with a running velocity at the population mean ( $v=2.3$  cm/s), maximum resource gain is achieved by building a circular web 32.5 cm wide. The mean adult web width in the field was 14 cm, with a



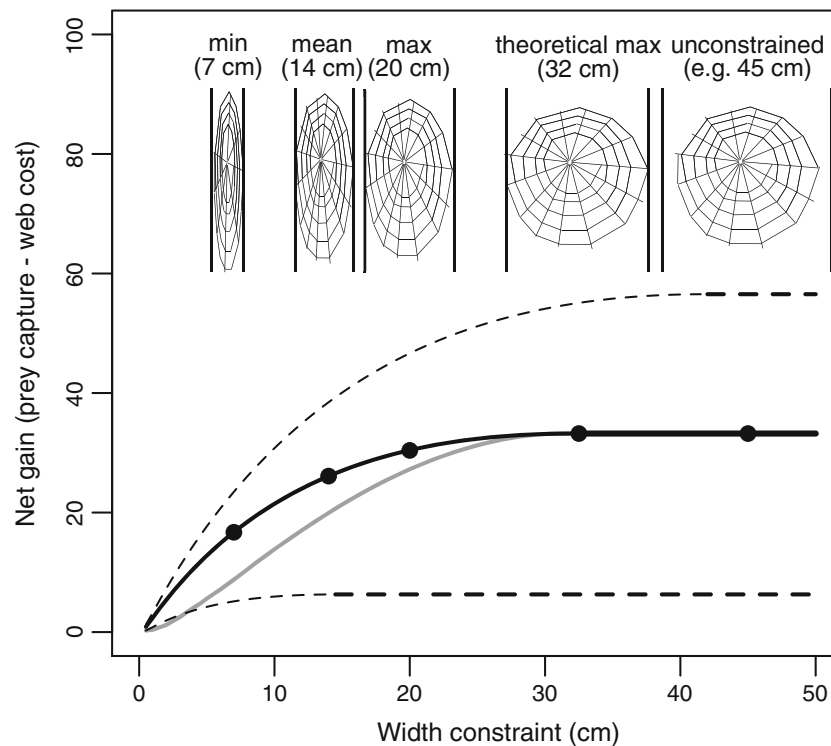
**Fig. 2** Predicted optimal **a** web elongation and **b** web area for maximum net resource gain at each of the width constraints modelled. *Solid lines* are predicted values when spider velocity equals 2.3 cm/s (mean velocity); *dashed lines* represent the range of spider velocities (min=1 cm/s, *lower line*; max=3 cm/s, *upper line*); *black circles* correspond to maximum potential resource gain at each velocity; *grey circles* are actual web elongation and areas, plotted against web widths, measured in the field ( $n=63$ )

predicted height to width ratio of 2.7 (height=38 cm). Therefore, compared to the predicted global optimal web (32.5 cm wide), a spider with an average web experiences a 21% reduction in net gain. For the minimum (7 cm) and maximum (20 cm) adult web widths in the field, height to width ratios are 5.6 (height=39 cm) and 1.8 (height=36 cm), which equate to reductions in net gain compared to the global maximum of 50% and 8%, respectively (Fig. 3). The model demonstrates that building webs in the space-

limited microhabitat on tree trunks reduces total resource gain achievable by *Telaprocera* spiders compared to building in a microhabitat without space constraints. Potentially, spiders could increase net resource gain by building wider, more circular webs on larger trees closer to the global optimum. However, any fitness advantage obtained by moving to a larger tree is likely outweighed by the considerable costs of moving (e.g. energetic costs and exposure to predators; Smith 2009). Furthermore, with poor vision and limited control over where they disperse to, there is no certainty that a new tree will be larger than the tree the spider moved from.

Clearly, building in space-limited conditions on tree trunks results in a reduction in maximum potential resource gain compared to building without space constraints. Nevertheless, by elongating their webs when space is in fact limited, spiders can achieve higher resource gain compared to building circular webs within the same space (grey line in Fig. 3). The advantage of web elongation increases as space becomes more constrained. In Fig. 3, it can be seen that for the narrowest webs measured in the field, the net resource gain for spiders with elongated webs is almost twice that for circular webs. Venner and Casas (2005) show that maximising web area increases overall prey capture rate and long-term survival and fecundity. For *Telaprocera*, web elongation allows spiders to maximise web area in a limited space, thereby maximising prey capture rate, probability of catching critical large prey, and therefore overall fitness. Strong selection to maximise prey capture potential and subsequent fitness is likely the main driver behind the high degree of behavioural plasticity that allows *Telaprocera* to adapt their webs to tree size.

Although *Telaprocera* spiders ameliorate costs of building on tree trunks by elongating their webs, the question remains why they evolved to build in this space-limited environment at all. Furthermore, given their high degree of behavioural plasticity when adjusting web shape, why are they so strictly arboricolous when deciding where to build? Building on tree trunks may protect ladder web spiders from hymenopteran predators, as the web forms a physical barrier preventing access to spiders hiding under the bark during the day. For instance, a New Zealand arboricolous ladder web spider, *Cryptaranea atriastula*, is parasitized less frequently than its sister species, *Cryptaranea subcompata*, which builds typical orb webs in the open (Forster and Forster 1985). Alternatively, tree trunks may provide a more stable building environment that reduces wind stress or web damage. *Telaprocera* appear to be generalist predators that catch diverse prey, and so building on tree trunks is unlikely to be an adaptation for targeting specific prey types (Harmer and Herberstein 2010).



**Fig. 3** Maximum net resource gain (prey capture–web cost) at each of the width constraints modelled. The *solid black line* is the predicted net gain when spider velocity equals 2.3 cm/s (mean velocity); *dashed lines* represent the range of spider velocities (min=1 cm/s, max=3 cm/s); the *solid grey line* is the maximum net resource gain if spiders built a circular web with the same horizontal diameter at each width constraint; *black circles* correspond to the web geometries in the top of

the figure. *Min*, *mean* and *max* are the minimum, mean and maximum web widths measured in the field and their corresponding web elongations. *Theoretical max* is the maximum achievable net gain and corresponding web geometry (circular) for spiders running at the mean velocity of 2.3 cm/s. *Unconstrained* demonstrates that beyond the theoretical maximum net gain, webs are unconstrained in space and should maintain the same size and geometry as webs at 32 cm wide

### Model limitations

Several factors were not included in our model that could potentially influence net resource gain. For example, we did not model the spacing of radial and capture spiral threads in the web. Spiders could reduce material costs of web elongation by increasing mesh spacing and reducing the cost  $c$  per unit area of web. However, mesh spacing is important in determining prey retention after interception, with finer meshes retaining prey for longer (Blackledge and Zevenbergen 2006). Reducing material costs by spreading silk more thinly may come at the cost of shorter prey retention times and lower prey capture rates. For laboratory-housed spiders (Harmer and Herberstein 2009), we found no correlation between web elongation and average mesh spacing ( $r=-0.23$ ,  $t_{37}=-1.41$ ,  $p=0.166$ ), suggesting *Telaprocera* spiders do not spread their silk more thinly when elongating their webs.

Increasing silk or web stickiness is potentially an alternative strategy to web elongation for increasing prey capture rates, but it is not a priori clear what the associated costs are. In principle, it might be optimal to vary stickiness within a web by increasing silk stickiness or by spacing

sticky threads closer together (to elevate capture rates in distant parts of the web or, alternatively, to maximize capture rates in the centre where the spider is able to reach most prey). However, evidence for such fine tuning of silk stickiness and mesh spacing to web architecture is lacking, and stickiness is therefore not included in our model. Furthermore, our model investigates the optimality of what *Telaprocera* spiders actually do in natural situations, which is to elongate their webs. Our model does not investigate the overall optimal prey capture strategy that a spider could potentially employ, and so including stickiness is not appropriate in this context.

Also excluded from our model was the probability of prey tumbling down the web. Some prey do not stick or escape immediately after interception, but tumble down the web as they struggle to escape (Zschokke et al. 2006). For *Scoloderus* that sit at the bottom of their webs, prey tumbling is a clear advantage as prey will always be tumbling towards the spider. However, in *Telaprocera* webs modelled here, spiders sit at the centre of their webs (Harmer 2009). We assume any advantage (i.e. increased prey capture) in reduced travel times, gained from prey tumbling towards a spider in the top web half, is nullified by increased costs of prey tumbling

away from them in the lower web half and therefore excluded prey tumbling from the model.

## Conclusions

Elongating their webs and deviating from the predictions of optimal central-place foraging clearly results in reduced resource gain for *Telaprocera* spiders compared to building webs without space constraints. Resource gain diminishes with available space as web area becomes increasingly constrained. However, spiders appear to minimise the cost of building in a space-limited microhabitat by building elongated webs, rather than circular webs, that maximise prey capture rate given the constraints of spider running speed. The high degree of behavioural plasticity that allows *Telaprocera* to adjust their web shape to the trees they build on is most likely an adaptation to building in these limited spaces, as there is strong selection to maximise resource gain. Our results have implications for understanding optimal foraging investment in other central-place foragers that experience space limitations in their foraging arenas, for instance, in ground-based foragers faced with physical barriers or flying foragers that share territorial boundaries with conspecifics.

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