

## Other ant invaders

In a recent *TREE* Perspective, Holway and Suarez<sup>1</sup> persuasively argued to integrate behavioral studies into research on ecological invaders. The authors highlighted provocative behavioral traits associated with invasive ants. However, the clear picture they paint is muddled by a more comprehensive survey of invasive ants. I agree wholeheartedly that behavior is necessary to understand invasions and, here, I strengthen the argument by reviewing significant links between behavior and invasive ant biology.

The authors reviewed the behavior of the two most-studied invasive ant species, the Argentine ant (*Linepithema humile*) and the red imported fire ant (*Solenopsis invicta*). In these two species, introduced populations are unicolonial, polygynous and generally lack intraspecific aggression. It is exciting to observe that in native habitats these behaviors are absent. Although this keen observation is useful, it is more powerful to use existing data on other well-known invasive species and to incorporate relevant discoveries.

Holway and Suarez remarked that '... detailed studies of other highly invasive ant species ... have yet to be done'. On the contrary, three other significant global invaders are known quite well: *Pheidole megacephala*<sup>2–5</sup>, *Wasmannia auropunctata*<sup>6–8</sup>, and *Solenopsis geminata*<sup>9,10</sup>. These species do not experience a radical shift in social behavior between native and introduced areas. *Wasmannia auropunctata* is unicolonial in native habitats, *S. geminata* is monogynous and monodomous in introduced areas, and it is likely that *P. megacephala* is unicolonial wherever it is native.

The native and introduced populations of invasive ants differ not only in behavior, but also in size and biogeography. Introduced populations of *W. auropunctata* have smaller-sized workers than native populations<sup>11</sup>. A broad survey of invasive ants shows that they are smaller in size than closely related non-invasive species<sup>11</sup> (T.P. McGlynn, PhD thesis, University of Colorado, 1999). Biogeography is also an important component of integrating behavioral observations. Indeed, a survey of all introduced ant species reveals that the most widespread species are unicolonial<sup>12</sup>. Also, some of the most widespread invasive species have extremely small worker sizes<sup>11</sup> (T.P. McGlynn, PhD thesis, University of Colorado, 1999). What are the connections between unicoloniality, small worker size, large geographic distribution, polygyny and the lack of intraspecific aggression? This is where the answers to proximate and ultimate questions are hiding. We do not have all of the answers yet, but behavior is clearly an important component.

**Terrence P. McGlynn**

Gettysburg College, Dept of Biology,  
Gettysburg, PA 17325, USA  
(tmcglynn@gettysburg.edu)

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## Relating populations to habitats

### Reply from D.A. Holway and A.V. Suarez

We are pleased that McGlynn agrees with the main point of our *TREE* Perspective article<sup>1</sup>, in which we argued that a full understanding of the success of animal invasions often hinges on a careful analysis of behavioral mechanisms.

McGlynn takes issue with our statement that '... detailed studies of other highly invasive ant species ... have yet to be done'. This is taken out of context. Other highly invasive ant species have been studied; however, in our Perspective article we acknowledge the value of detailed behavioral studies, specifically those that compare introduced with native populations<sup>2–4</sup>. His statement that '... three other significant global invaders are known quite well', is not supported by his citations, which focus primarily on introduced populations or do not address mechanisms explaining invasion success.

Our point is well illustrated by McGlynn's own example of a 'well studied' species, *Pheidole megacephala*. Although *P. megacephala* is a widespread invasive species<sup>5</sup>, little is known about the mechanisms underlying its ecological success or whether differences in social structure exist between native and introduced populations. This uncertainty is illustrated by McGlynn's own statement: '... it is likely that *P. megacephala* is unicolonial wherever it is native'.

In addition, McGlynn makes several unqualified statements about the red imported fire ant (*Solenopsis invicta*). First, *S. invicta* occurs in two social forms in its introduced range; the widespread monogyne form is multicolonial, monogynous, and exhibits pronounced intraspecific aggression<sup>2,6</sup>. Second, although *S. invicta* and *Linepithema humile* have undergone behavioral shifts following introduction, McGlynn's statement that traits such as polygyny are absent from native populations is incorrect<sup>2,3</sup>.

**David A. Holway**  
**Andrew V. Suarez**

Dept of Biology – 0116,  
University of California, San Diego,  
9500 Gilman Drive, La Jolla, CA 92093–  
0116, USA (dholway@biomail.ucsd.edu;  
asuarez@biomail.ucsd.edu)

In a recent *TREE* review, Boyce and McDonald<sup>1</sup> demonstrated how resource selection functions<sup>2</sup> (RSF) can be used to calculate the probability of habitat use, which 'is useful because we can simply sum the probabilities of use over an area to estimate total population size'<sup>1</sup>. RSF are typically estimated using availability data versus use data<sup>1,2</sup>, assuming that use is directly proportional to availability<sup>3</sup>. Boyce and McDonald<sup>1</sup> acknowledge that differing habitat availability might be a problem at a study area scale; and that the value of habitats is not necessarily based upon their use because, for example, habitats used for sleeping might not be in short supply nor be crucial for survival<sup>4</sup>. To solve these problems, they suggest that RSF must be calculated for each study area and that each habitat could be given a caloric value for the food resources. These problems were mentioned separately, but are actually closely intertwined. Animals often use different habitats for different activities or time periods, and therefore habitat use might not be directly proportional to habitat availability even at a within study area scale<sup>3</sup>.

Recently, we reanalyzed the data set of Aebscher et al.<sup>5</sup> on grey squirrels (*Sciurus carolinensis*) that were foraging in grain fields with abundant food but poor protective cover, and seeking shelter in adjacent forest habitats with cover but less food<sup>3</sup>. Within this study area, individual grey squirrels selected grain fields when the availability of grain fields within their home range was less than 10%, whereas they selected against grain fields when the availability was above 10%. Thus, selection for a particular habitat was conditional on the relative availability of other habitats – what was termed a functional response in habitat use<sup>3</sup>. No other formal analysis has been conducted to search for functional responses in habitat use in other organisms. However, because different trade-offs in foraging between energy intake and, for example, predation risk have been demonstrated for a number of different organisms, including birds, mammalian carnivores and cervids<sup>3,6,7</sup>, functional responses in habitat use are probably common. Because use might vary with habitat availability at the within study area scale<sup>3</sup> and also with distance to habitat border zones<sup>8</sup> ('edge'), giving habitats caloric values cannot solve this problem. Thus, there are numerous