

Other ant invaders

In a recent *TREE* Perspective, Holway and Suarez¹ 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*²⁻⁵, *Wasmannia auropunctata*⁶⁻⁸, and *Solenopsis geminata*^{9,10}. 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 populations¹¹. A broad survey of invasive ants shows that they are smaller in size than closely related non-invasive species¹¹ (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 unicolonial¹². Also, some of the most widespread invasive species have extremely small worker sizes¹¹ (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.

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

We are pleased that McGlynn agrees with the main point of our *TREE* Perspective article¹, 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 populations²⁻⁴. 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 species⁵, 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^{2,6}. 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^{2,3}.

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Relating populations to habitats

In a recent *TREE* review, Boyce and McDonald¹ demonstrated how resource selection functions² (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'¹. RSF are typically estimated using availability data versus use data^{1,2}, assuming that use is directly proportional to availability³. Boyce and McDonald¹ 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 survival⁴. 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 scale³.

Recently, we reanalyzed the data set of Aebischer et al.⁵ 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 food³. 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 use³. 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^{3,6,7}, functional responses in habitat use are probably common. Because use might vary with habitat availability at the within study area scale³ and also with distance to habitat border zones⁸ ('edge'), giving habitats caloric values cannot solve this problem. Thus, there are numerous

cases when simple, proportional RSF cannot be used to give reliable population estimates.

In the case of a trade-off situation between two habitat types, functional responses in the use of one habitat versus the other can easily be modeled by applying standard, generalized linear models or specifically tailored non-linear models to use data versus availability data³. The more complex situation when such a trade-off involves more than two habitat types has not yet been explored. We agree with Boyce and McDonald¹ that the theoretical foundation for habitat ecology is still weak. However, more explicit considerations about expected functional responses in habitat use under different constraints, for example, predation risk, time and energy budgets, might improve this unhappy state of affairs.

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Reply from M.S. Boyce, L.L. McDonald and B.F.J. Manly

We strongly support the assertion of Mysterud and Ims¹ that resource selection function (RSF) models² can depend on the availability of resources. This point might apply at any spatial scale³, not just for the selection of habitats within a home range. However, in some populations RSFs are independent of availabilities, as we explained in our review⁴. Understanding why and how selection changes when availability changes is an important problem.

We also concur with Mysterud and Ims¹ that building overly simplistic RSF models could be naïve because of complex behaviors and interactions between resource requirements. One of the strengths of the RSF approach for modeling habitat selection is that it easily accommodates such complications. We believe that habitat selection seldom can be sufficiently characterized using only two habitat types, as in the two examples offered by Mysterud and Ims⁵. There are

no barriers to the development of models relating multivariable RSFs to availability. Examples with more than two prey types have been published⁶, for example, for rudd (*Scardinius erythrophthalmus*) feeding on the aquatic hemipteran *Sigara distincta*⁷. Such RSFs for selection of a prey type can be readily applied to habitat selection. We explicitly reviewed⁴ an alternative approach where RSFs can be constructed for each individual's home range; a general RSF can then be obtained by modeling RSF coefficients (as response variables) as a function of availabilities. This is a more general and more flexible approach than estimating a 'habitat functional response'⁵.

We take issue with the suggestion that using RSFs assumes that use is proportional to availability^{4,5}; if this were so, animals would be showing no selection whatsoever. As Mysterud and Ims¹ point out, habitat use patterns are seldom proportional to availability. We recognize that our contention relates to different definitions of availability. Given the spatial scale defined by Mysterud and Ims⁵, we assume that availability refers to the total or mean resources available within an individual's home range. But, regardless of the availability definition, RSFs generally are not proportional to availability – RSF modelling is flexible and virtually any function can be used as long as the model is proportional to the probability of a resource unit being used. As indicated by Mysterud and Ims⁵, one can easily incorporate polynomial or nonlinear functions into an RSF where the RSF is not proportional to availability. Indeed, an RSF is constructed for a particular availability regime², and the issue in question is whether varying the availability alters the RSF. Indeed, sometimes it does.

Mysterud and Ims¹ make reference to our suggestion that an index of habitat importance, based on caloric value, can be calculated. This is taken out of context. Although it might be worthwhile to have such an index of the food value of various habitats, such an index is not an RSF and cannot be used to extrapolate population size.

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The behavior–conservation interface

Caro¹ summarizes the many areas of conservation management that could benefit from explicit, quantitative application of behavioral research. However, contrary to his statement '... use of behavioral knowledge has never been expounded by the behavioral community or explicitly recognized by conservation biologists'¹, the idea of using behavioral understanding to inform conservation management has been around for a long time. For instance, *The Behaviour of Ungulates and its Relation to Management*, a two-volume compendium of >50 papers edited by Geist and Walther was published a quarter of a century ago².

Caro¹ listed several areas where ethology could be applied to conservation: fragmentation, responses to exploitation and disturbance, effective population size, captive breeding and reintroductions, monitoring and predictive tools, human behavior, and the future of behavioral research for conservation. Twenty-two of the 31 chapters in Volume 2 of Geist and Walther² explicitly address one or more of these areas; the only missing topic is disease, but then Caro also missed the important topic of using ethology to predict animals' effects on the habitat.

Ignoring previous work is, of course, a prescription for wasting resources on reinventing the wheel. Although our ability to apply ethology to conservation management has improved over the past 25 years^{3,4}, I suspect that in some areas the improvement is not so great now that the shoulders of bygone giants are unhelpful. Perhaps a good student project would be to compare the recent flurry of compendia on the topic of the behavior–conservation interface⁵ to Geist and Walther², to specify just where advances have, and have not, been made, so that our use of precious conservation resources could be spent more efficiently.

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