Other ant invaders

In a recent TREE Perspective, Holway and Suarez1 persuasively argued to integrate behavioral studies into research on ecological invaders. The authors pointed out that "...the lack of intraspecific aggression? This is exciting to observe in 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 megacephala4–5, Wasmannia auropunctata6–8, and Solenopsis geminata9,10.

The native and introduced populations of W. auropunctata have smaller-sized workers in size and biogeography. Introduced populations of W. auropunctata have smaller-sized workers than their native populations11. A broad survey of invasive ants shows that they are smaller in size than closely related non-invasive species12. TMC 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 where the most widespread species are unicolonial13. Also, some of the most widespread invasive species have extremely small worker size13. T.M.C McGlynn, PhD thesis, University of Colorado, 1999: What are the connections between unicolonialism, small worker size, large geographic distribution, polygyn 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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References

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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 populations3. His comment that ‘... three other significant global invaders are known quite well’, is not supported by his citations, which focus primarily on studies about the red imported fire ant (Solenopsis invicta). In these two examples, introduced populations are unicolonial, whereas 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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References

Relating populations to habitats

In a recent TREE review, Boyce and McDonald1 demonstrated how resource selection functions (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 size3. RSF are typically estimated using availability data versus use data4, assuming that use is directly proportional to availability. Boyce and McDonald acknowledged that selecting habitat availability might be a problem at a study area scale; and that the value of habitats is not necessarily based upon availability, but rather, the importance of habitats for the food resources. These problems were mentioned separately, but are actually closely intertwined. Animals often use different habitats for different activities over time periods, and therefore habitat use might not be directly proportional to habitat availability even at a within-study area scale.

Recently, we reanalyzed the data set of Adisch et al.5 on gray 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 food6. 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 adjacent forest fields when the availability of grain fields was above 30%. Thus, selection for a particular habitat was conditional on the relative availability of other habitats – what we termed a functional response in habitat use. 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 corvids7–9, functional responses in habitat use are probably common. Because use might vary with habitat availability at the within-study area scale and also with distance to habitat border zones ('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 this 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 data. 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 McDonald 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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References

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

We strongly support the assertion of Mysterud and Ims that resource selection function (RSF) models can depend on the availability of resources. This point might apply at any spatial scale, 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 review. Understanding why and how selection changes when availability changes is an important problem. We also concur with Mysterud and Ims that building overly simplistic RSF models could be naive 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 Ims. There are no barriers to the development of models relating multivariate RSFs to availability. Examples with more than two prey types have been published, for example, for rudd (Scardinius eryophthalmus) feeding on the aquatic snail Lymnaea stagnalis. Such RSFs for selection of a prey type can be readily applied to habitat selection. We explicitly reviewed 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. We take issue with the suggestion that using RSFs assumes that use is proportional to availability; if this were so, animals would be showing no selection whatsoever. As Mysterud and Ims pointed 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 Ims, 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 modeling 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 Ims, 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 regime, and the issue in question is whether varying the availability alters the RSF. Indeed, sometimes it does.

Mysterud and Ims 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 expended by the behavioral community or explicitly recognized by conservation biologists2”, 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 ago. Caro 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 Walther 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 animal 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 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 interface4 to Geist and Walther, 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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References