Journal Club

Why didn't I think of that? Avian nest predation and parental activity

Every so often, a hypothesis comes along that contains an idea that makes you wonder why no one has thought of it before. A recent paper by T.E. Martin *et al.*[1] contains such a conceptual leap.

In 1949, A.F. Skutch provided an original hypothesis regarding the evolution of parental care behaviour in birds. The hypothesis was that nest predation should increase with increasing parental activity at the nest, thus predicting that parental activity and nest predation show opposite proximate and evolutionary relationships. That is, nest predation is expected to increase with parental activity within species to give a positive proximate cost function, and species or populations in environmental conditions with higher ambient levels of nest predation should evolve lower parental activity, giving a negative evolutionary function across species or populations. There is much support for the negative evolutionary pattern, but apparently little support for the proximate relationship.

In line with several previous studies, Martin *et al.*[1] found that nest predation was no greater during the nestling period than it was during the incubation period, when flights to and from the nest were fewer. This same pattern was seen in all of ten species studied. Previous workers had concluded that results of this kind argued against a proximate cost function between nest predation and parental activity: if increased parental activity during the period when nestlings need to be fed produces no significant increases in predation risk, then it seems unlikely that there should be selection to reduce parental provisioning rates. The great insight of the current work, however, is to see that such conclusions assume that parental activity is the dominant influence on the predation risk of a nest and, in particular, that the site of an individual nest does not influence its risk of predation. By using baited nests from the previous year whose predation history was known, Martin *et al.* show that the location of a nest has very clear effects on nest predation rates – nests that had a high risk of predation in one year also had a high risk in the subsequent year. Thus, high initial predation rates on easy-to-find nests should cause a higher predation rate during the incubation period than during the chick-rearing period (when predators have found most of the nests in vulnerable sites). The fact that neither Martin *et al.*'s study, nor the previous works found such an effect suggests that some other factor (which the authors assume is parental activity) provides a compensatory increase in predation rates during the chick rearing period. Under this paradigm, the commonly reported lack of difference in predation rates between incubation and chick-rearing periods switches from failing to support Skutch's hypothesis, to providing strong support for it. Further evidence in support of the authors' explanation comes from a nonground nesting bird, the hermit thrush, *Catharus guttatus*, which shows similar parental activity between the incubation and nestling periods, and which showed higher nest predation rates during the incubation period.

Suddenly, predation risk is looking like an important evolutionary influence on the evolution of parental care (in birds at least). Exploration of the tradeoff faced by parents wanting to minimize drawing the attention of predators to their young while still satisfying their provisioning needs should be a very productive line of research.

1 Martin, T. E. *et al.* (2000) Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc. R. Soc. London B Biol. Sci.* 267, 2287–2293

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Nectar, nodules and cheaters

Parasitism or mutualism, which is it? Or, as a few authors have suggested, are mutualisms simply reciprocal parasitisms between individuals of two interacting species? The tendency to cheat among partners that usually make an investment in the mutualistic relationship has recently been highlighted. Why don't mutualisms dissolve because of cheating? Although some mutualisms probably do dissolve because of this inherent tendency, some mutualists do not rely on benefits that require an investment from partners. For example, honeydew might be a free by-product of aphid feeding that is food for mutualistic ants. With such benefits, cheating is not an issue. Investments, however, are made in many mutualistic relationships. Pioneering theory by J.J. Bull and W.R. Rice and empirical work by O. Pellmyr and colleagues previously demonstrated that partner choice or retaliation against noncooperative partners could lead to the evolutionary stability of mutualisms. Two new papers[1,2] now add to our understanding of how cheating influences the ecology and evolution of mutualisms by addressing the natural history and patterns in two common associations: legume–rhizobia interactions and nectar robbing of flowers by insects.

Denison[1] discusses the symbiotic and apparently mutualistic relationship between plants in the family Fabaceae (legumes) and nitrogen-fixing bacteria (rhizobia). Although this association has been a textbook example of mutualism, it is, in many ways, a mystery. First, rhizobia inside nodules on plant roots are often reported to be nonfree-living bacteria incapable of reproduction. Second, partner choice by legumes at the time of infection must be made without reliable information on cost : benefit differences among rhizobia strains, none of which will fix nitrogen for several days. Denison offers detailed natural history in an evolutionary framework allowing us to reassess this

association: (1) most nodules contain reproductively viable rhizobia, even in legume species where nonreproductive 'worker rhizobia' actually fix the nitrogen; and (2) plants can potentially attack, stop feeding, or asphyxiate uncooperative nodules. Maloof and Inouye[2] address a similarly fundamental question for nectar robbers, typically thought of as cheaters of plant–pollinator mutualisms. Their review of the literature across many taxa in space and time indicates that nectar robbers have a negative effect on plant fitness in only one third of the studies. Do all nectar robbers have a negative effect on plants under certain conditions? It might be so, but Maloof and Inouye's synthesis suggests that these conditions are somewhat restrictive. In addition, the intriguing finding that plants sometimes benefit from nectar robbing is reminiscent of 'overcompensation of plants in response to herbivory' and requires further

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investigation and hypotheses. Under what ecological conditions does parasitism switch to mutualism?

Although these papers make important contributions, further reviews and the development of novel theory are needed to develop a synthesis of why and when mutualism is not parasitism. Some of the fundamentals of our textbook examples of mutualism are holey. Do we know enough of the natural history? I say no. Do we understand the ecological conditions that make apparent cheaters not so bad? No. Are mutualisms really balanced reciprocal parasitisms? Sometimes.

1 Denison, R.F. (2000) Legume sanctions and the evolution of symbiotic cooperation by rhizobia. *Am. Nat.* 156, 567–576
2 Maloof, J.E. and Inouye, D.W. (2000) Are nectar robbers cheaters or mutualists? *Ecology* 81, 2651–2661

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Trading space for time in population dynamics

Classic models, such as the Lotka-Volterra or the Nicholson–Bailey, assume that we can understand the dynamics of populations without worrying about the fact that interactions between individuals are played out in space. These models were developed using the analogy to the 'mass-action' interactions between molecules in a volume of gas. An analogy that is without-a-doubt an attractive one, because the subsequent half-century of theoretical ecology stuck faithfully to that particular line of reasoning. The apparent take-home message appeared to be that population dynamics can be understood as a fairly low-dimensional system, and allowance need not be made for the spatial component to dynamics. The advent of modern computer power, however, has raised doubt about the validity of this assertion, because numerical simulations provide mounting evidence that space is indeed important. The direct implications are graver than we tend to acknowledge, because dynamical systems theory (see, for example, Taken's theorem for prediction in deterministic systems and the Cayley–Hamilton theorem for stochastic systems) says that the number of time lags involved in regulation should scale with the number of interacting populations. [Theoretically speaking, therefore, the regulation of a population embedded in a predator–prey metapopulation with ten subpopulations should involve studying

~10–20 lags of regulation.] Acknowledging space would hence seem logically to imply abandoning any hope of having simple low-dimensional rules for population dynamics. For theorists dabbling in spatiotemporal dynamics, it is only human to have the left hand ('space') ignore what the right hand ('time') is doing.

Keeling and co-workers[1] have now published what might promise to provide an elegant way for theoretical ecology to both have the cake and eat it. They study two different predator–prey metapopulation models where local dynamics follows Lotka–Volterra dynamics. The patches are linked through global dispersal of both the predator and the prey. The dynamics of this spatial system differ from its nonspatial analogue in being more stable. The stability arises because the limited movement (only a fraction of the individuals move) induces spatial association between the two species. Using moment techniques – a mathematical modeling technique for stochastic systems that involves writing down a sequence of equations for the mean, the variance, the skewness, etc.– the authors show that simple equations can still be used to understand the aggregate dynamics. The trick is to include a correction factor for the interspecific covariance in the equation for the mean. Similar results have been obtained from previous applications of moment equations[2]. Keeling *et al.*, however, go one

exciting step further by developing an explicit approximation for the covariance, as a delayed density-dependent function of the mean. This demonstrates that the complex spatiotemporal interactions in a parasitoid–host metapopulation can, if care is taken, be modeled using low-dimensional rules. In the example developed by Keeling *et al.*, this results from trading in the slightly simplistic spatial dynamics (global dispersal within the metapopulation for all individuals that disperse) for one additional density-dependent lag in regulation. My personal enthusiasm for this work is, first, for the results themselves. I am also excited about the new theoretical road that is opening. I envisage a theory, incorporating localized dispersal, that trades off spatial interactions for temporal lags in a fashion orders-of-magnitude more economic than that of Taken, Cayley and Hamilton, and closes our much denied gap between spatial and temporal theories of population dynamics.

1 Keeling, M.J. *et al.* (2000) Re-interpreting space, time lags and functional responses in ecological models. *Science*, 290 1758–1761
2 Bolker, B. and Pacala, S.W. (1999) Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *Am. Nat.* 153, 572–602

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