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COMMENTARY

HABITAT SATURATION AND ECOLOGICAL CONSTRAINTS: ORIGIN AND HISTORY OF THE IDEAS

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Lawton suggests that my book, *Helping and Communal breeding in Birds,* "must be fascinating to sociologists of science" because the book received favorable reviews in *Science, Nature,* and *American Scientist* (to which could be added, *Animal Behavior, Trends in Ecology and Evolution, Journal fur Ornithologie,* and others) but "embarrasses" some of her anonymous acquaintances who work in this area. Using Hull's concept of conceptual lineages and literature on delayed breeding, she argues that I have not credited certain unspecified workers adequately. Lawton's extreme accusations concern matters that are centrally important in the history of the ornithological study of helping behavior and that apparently need further clarification. Therefore, I accept her invitation to comment.

I agree with Lawton that in the literature on helping there is ample material for a fascinating study of how lineages of ideas evolve, but I would go further in two ways. First, I would invoke another of Hull's favorite ideas, namely that the self-serving behavior of politically influential scientists interacts importantly with the history of ideas. Her review reflects political promotion at the expense of the truth by some of her colleagues over the last decade or more. I argue that this promotion, whether by self or friends, retards science and that good scholarship can reveal and correct its effects.

Second, when we examine the conceptual lineages relevant to helping, we find that there are lineages that arise from mistakes and misrepresentations as well as lineages of good ideas, ones that result in genuine progress. As it turns out, the "bad" lineages shed considerable light on the good ones and how they are perceived by outsiders. In my commentary on this "social scene" conjured up by Lawton, I must first describe some dying lineages, because the resulting perspective clarifies the history of the concept of ecological constraints, her prime example.

Before going on, however, I would like to say that the published reviews of *Helping* were not written by naive, unqualified people as Lawton implies, insulting these reviewers in the process. They included prominent researchers who have made important contributions to the study of helping, such as Orians (1987) and Curry (1988), as well as others who are excellent avian behavioral ecologists, i.e., Ewald (1987), Patterson (1987), and Petrie (1989). The dichotomy claimed by Lawton, that the positive reviews are by naive outsiders, while true insiders are uniformly negative, does not stand up to examination, nor will it, I predict, when more ornithological journals get around to their reviews.

Furthermore, it should be realized that several of the researchers presumably consulted by Lawton already had unreasonably strong negative emotions about me well before publication of *Helping.* Their reasons possibly included the following: (1) that I had pointed out their errors in print, (2) that I insisted on regarding indirect selection as part of a viable hypothesis even though it was extremely unpopular among ornithologists, (3) that I employed the experimental method and advocated its use while others denigrated it, (4) that I employed the method of rejection of alternative working hypotheses, and complained that its lack of use by others was delaying progress, and (5) that I took mathematical theory seriously. These individuals can hardly be considered to be unbiased judges of *Helping.* One was so hot under the collar in 1985 that he vowed never again to read anything I wrote. Presumably, he has not even read the book and would refuse to review it. Negative grumbling from these individuals is to be expected. It is absurd for Lawton to suggest that they are the only people qualified to comment on *Helping.* It is not even clear that they have read the book.

In writing *Helping* I attempted to review all the theory and data ever published on the subject following the logic of science and the traditions of scholarship. I tried not only to cite *every single paper ever published* on the subject but also to describe fairly and accurately every significant new contribution to the logical progression of ideas, whether factual or theoretical.

To minimize errors and bruised egos I asked many people to comment on prepublication drafts and many did. Prominent among those who declined to review *Helping* for me are some of the people to whom I believe Lawton refers as having refused to review the book for her. My attention to completeness and accuracy has been praised by neutral reviewers but to Lawton, "Brown's book is characterized by an almost universal failure to grant credit to other workers. . . ." She provides no specific verifiable examples. Why is Lawton's opinion so different from that of all other reviewers?

When one has literally lived much of the history of the field and scrutinized every paper over a 30-year period as it was published—as I did—one obtains a different perspective than that of the hallway conversation at recent bird meetings, Lawton's milieu. It should not be surprising that some people seem to be suffering cognitive dissonance. Casual conversations can easily be superficial, misinformed, self-serving, and unreliable. A study of the retarding effects of published misinformation on the progress of science, especially when propagated in cliques of reciprocal flatterers, would richly repay a sociologist or historian of science in this area. I stand ready to assist him/her by providing information that cannot be related here.

Returning to Hull's selection analogy, there must also be conceptual lineages that have been selected against. A good example of an unfit conceptual lineage and of how errors lead to misplaced recognition is the suggestion of Woolfenden and Fitzpatrick (1978a) that nonbreeders "help" (i.e., delay breeding and dispersal) in order to get a territory. As they presented it the hypothesis seemed at first to offer a new and persuasive alternative to indirect kin selection; and consequently the authors received much undeserved credit. As I have explained in Brown (1978b), in *Helping,* and in my (1987b) review of Woolfenden and Fitzpatrick (1984), there are several problems. It was a misrepresentation by them to claim this as a new idea because I had already argued that birds choose to be nonbreeders to get a territory in the future (Brown 1969a, 1974, 1975) as had Selander (1964) independently. It was a major misrepresentation by them of the central scientific issues to claim that I had invoked simply "kin selection' to explain delayed breeding and dispersal, since I had actually invoked *ecological constraints* (without kin selection) when I argued that reduced dispersal "in an environment continuously at carrying capacity and with few suitable vacant territories . . . sets the stage" for indirect selection to favor helping (Brown 1974). Later (1987a) I finally realized that the reason Woolfenden and Fitzpatrick continued to repeat these errors even though they had been repeatedly brought to their attention (e.g., Brown 1978b) was quite likely that they were confounding the causes of nonbreeding with the causes of helping by treating them as being identical. Because they identified presumed helpers operationally by the incorrect criterion of nonbreeding status, they were continually misunderstanding the literature and misleading readers and audiences. This bewildering collection of misinformation repeated to many audiences over a decade led to unproductive debate, misunderstanding, and polarization of the field that is still evident in Lawton's gripes.

These mistaken practices were soon adopted by the Berkeley group studying Acorn Woodpeckers and were also picked up by Emlen (1982, 1984) where a helper is implicitly assumed incorrectly to be a nonbreeder. Recently, this "bad" conceptual lineage began to go extinct when Koenig and Mumme (1987) finally, after considerable cajoling from me, explicitly renounced these practices. Clearly, if anything was "done by mirrors," as stated by Lawton, it was by the above authors—not by me. The truth can come as a shock when one is accustomed to something else.

A focus of Lawton's ire is my treatment of territorial behavior and the resultant habitat saturation as an ecological constraint that might be partly responsible for delayed breeding and dispersal. In the pages to which she refers, I used a well-known model of mine to illustrate the general idea of saturation and then briefly showed how I used this model in 1969a to explain delayed breeding, delayed dispersal, group territoriality, and helping. When introducing these very simple ideas, my purpose was to explain the concepts clearly, not to flatter later authors who simply repeated or embellished them in minor ways. There is extensive coverage elsewhere in *Helping* of the relevant work of the authors mentioned by Lawton.

What the anonymous persons mentioned by Lawton seem to have wanted was to receive credit for the origin of the ideas. But why should they be credited in this context? They did not originate the basic ideas, nor participate in their early development, nor does Lawton mention any significant addition to the ideas by these authors or other important contributions that I failed to mention.

Lawton's history is simply wrong. She writes, "Brown then goes on to present his model as though he is the first worker to have developed such a construct. He tells us nothing of the twenty-year history. . . ." The published record shows that the graphical model I presented (fig. 5.5 in *Helping*), which was first published in 1969b, really was the first such model. Obviously, it predates the 20-year history to which she refers. I acknowledged, as I always have, that Selander (1964) was the first to describe the idea of habitat saturation in relation to helping. (I learned of his truly obscure comments only because he reviewed my manuscript before publication.) Nevertheless, I did develop the idea independently, more generally, and in several publications. Thus, I did *not* "co-opt ideas" of others, as Lawton alleges. My ideas on this subject were expressed in 1969a, 1974, and 1975 (p. 207), well before the claims of my rivals, as well as repeatedly since then. Agreeing, Woolfenden and Fitzpatrick (1978b) wrote, "Selander and Brown have indeed hypothesized that certain animals delay reproduction and remain in the parental home area as a means of obtaining space for breeding." They belatedly pointed out that their contribution in 1978a was not the above idea but what I have called the augmentation hypothesis, for which Woolfenden and Fitzpatrick receive full credit in *Helping.* Emlen (1982) also acknowledged Selander (1964) and Brown (1974).

As if realizing the weakness of her argument based on priority, Lawton then takes the different tack of saying that my 1969a treatment was anyway ridiculously obscure. She parodies it with an analogy between the "obscurity" of this paper published in the *Wilson Bulletin* and the obscurity of a comment on natural selection published in *Naval Timber and Arboriculture.* The comparison is absurd. The 1969a paper was at the time the major review of the concept of habitat saturation and its role as an ecological constraint in populations of birds. In the early and mid-1970s no ornithologist interested in territorial behavior as an ecological constraint would have missed it. The mathematical model developed in the 1969a paper was the basis for its graphical version in 1969b, which is the model to which Lawton refers (fig. 5.5 in *Helping*). This was one of the few works cited by the Brewster Medal committee to justify their award. These two 1969 papers on territoriality, habitat saturation and the ideal free distribution (then called the optimal mix) received good numbers of citations for their day, and the illustration is still used in textbooks. Even though this well-known paper (Brown 1969a) was not cited by Woolfenden and Fitzpatrick (1978a), they undoubtedly read similar ideas in my 1974 paper on the evolution of helping in jays (which they did cite) and could have read them in my textbook (Brown 1975). Other workers at the time recognized the importance of these early writings on ecological constraints (Stacey 1979). The only possible rival claim is a short passage in the article in *Bioscience* by Woolfenden and Fitzpatrick (1978a) mentioned above which gave no credit at all to anyone else. Most likely, Woolfenden and Fitzpatrick had both read all three of my treatments of the subject.

The conceptual lineage goes as follows: Selander (1964) and Brown (1969a) originated the ideas independently. Brown (1974, 1975, p. 207, 1978a, etc.) integrated them with current ecological and evolutionary theory. Woolfenden and Fitzpatrick (1978a) probably read them in Brown's 1975 book or papers, as did Stacey (1979), who acknowledged Brown (1974). Koenig and Pitelka (1981) acknowledged Brown (1974) and used Brown's (1969a, p. 314–315) idea of group territoriality and helping as a "last resort" strategy using the same words without acknowledgment. They faithfully replicated the characteristic errors of Woolfenden and Fitzpatrick (1978a), again presenting their ideas incorrectly as being in opposition to mine. Emlen (1982) overlooked Brown (1969a) but cited Brown (1974), using some of the same words, e.g., "setting the stage," the same mathematical formulation as Brown (1978a), and many of the same ideas, in some cases without acknowledgment.

Of course, habitat saturation cannot by itself explain delayed breeding and dispersal. For example, Brown (1969a) cited many examples of a population surplus in species lacking nonbreeding helpers. Therefore, in 1969a he restricted the habitat saturation hypothesis to species in which "first year birds sometimes linger in the territories of their parents" and he later developed the hypothesis that "individuals can use helper status as a stepping-stone to breeding status either in their own or a neighboring territory" (Brown 1978a, p. 135). He also argued that delayed dispersal would be favored when survival was higher for a nonbreeder in its natal territory than in some other place or habitat (Brown 1978a), an idea adopted by Koenig and Pitelka (1981) without acknowledgment. Furthermore, the foraging energetics of group territoriality and feeding of young must be considered as a factor that may interact with habitat saturation (Brown 1969a, 1982), an idea picked up by Gaston (1978) without acknowledgment. All of these ideas, which originated in these or other earlier papers, have been claimed incorrectly by later authors as their own original contributions. I could document these points and provide several further examples, but I think I have already made my point that later authors have been careless or even irresponsible about ignoring or misrepresenting earlier ones. I believe that the persistent misrepresentation of early papers by later authors named elsewhere in this paper has encouraged authors and reviewers to overlook the facts.

What possible motive could there be for this campaign of misinformation by Lawton and the strange, continuing misrepresentation of the scientific issues by Woolfenden, Fitzpatrick, and their followers? Does their repeated and knowing use of my ideas on ecological constraints in their public lectures without acknowledging their true origin give anyone a right to assign credit to them for their origin and development? To Lawton and her anonymous nonreferees, yes; in the verifiable history of ideas, no.

Lawton states that the study of ecological constraints on breeding is a productive area today. It does receive attention, but it is not clear how productive of genuine progress this has been. The same basic ideas used in the 1960s and 1970s by me are still being repeated today using different jargon (e.g., "ecological constraints"), but I have not seen significant development of the theory. Empirical support is also little improved since 1969. New facts consistent with the old ideas continually appear, but alternative hypotheses remain unrejected. For further comment on this, see *Helping.*

We may now return to the sociological aspects of the cognitive dissonance which Lawton has tried to explain. The contrast between what some people have come to expect from casual conversations with colleagues and what a scholarly examination reveals centers on two papers. Both papers were well received by readers with a bias for viewing the main issue as a dichotomous choice between ecology and genetics and a preference for ecology because they tended to reinforce the bias. The issue is not so simple. Both papers claimed to have presented new and exciting theory, yet in each case the allegedly new ideas can be found in papers that are cited by the authors. The authors in both cases have been most reluctant to admit their errors (though they are acknowledged by others), and their supporters seem to have more interest in partisan politics than in careful scholarship.

I have discussed above the first case in some detail. Summarizing, Woolfenden and Fitzpatrick (1978a) were favored by a readership that wanted the issue to be presented simply as ecology vs. kinship without complications. The scenario presented was deceptively simple and pleasant for this readership, but the scholarship and logic were seriously flawed as I have indicated. The sociological effect of this misinformation and drastic oversimplification is still with us, as Lawton's comments show.

By 1982 readers who accepted the oversimplified picture that had come from the Scrub Jay authors were ready for this view to be generalized. Emlen (1982) did this by joining the already long familiar ecological mechanisms for delayed breeding (i.e., habitat saturation, excess males) under the umbrella jargon of "ecological constraints." He contended that one of these, food shortage, was new. It was not. The food shortage theory had been clearly described already in a paper in Emlen's bibliography (Orians et al. 1977). In short, Emlen's paper contained major new jargon but not major new ideas. The few data were not fully presented, and their interpretation remains ambiguous. Shortcomings of this paper are discussed in *Helping.* Emlen then paid little attention to the method of alternative, rejectable hypotheses; consequently, little progress was actually made. The paper by Emlen and Vehrencamp (1983) that Lawton holds up as a model of scholarship is derived mainly from the 1982 papers and is, therefore, largely unoriginal. The 1985 paper is virtually a word-for-word reprint of most of the 1983 paper. These papers received little attention in *Helping* because of their derivative nature.

My estimation of the contribution of these papers to the progress of science certainly differs from that of Lawton and the anonymous individuals she has consulted, as discussed extensively in *Helping.* I submit that the popularity of these papers and some others for Lawton and her nonreviewers derives primarily from sociological factors. These papers appeared to uncritical readers to present important new ideas, but for careful readers familiar with the literature they did not; they repeated old ideas in new words, often without acknowledging sources. They appeared to resolve complexity into simplicity; but this was deceptive, as shown in *Helping*. They strengthened existing biases uncritically.

Finally, I regret to note that Lawton's entire review is devoted to the ego satisfaction of a few colleagues. She does not raise even a single genuinely scientific idea worthy of discussion, nor does she present verifiable facts to support her exaggerated claims. Her documentation consists primarily of private comments from anonymous persons each of whom declined to write a review and may not have read *Helping* at all. In my opinion the study of helping has suffered from too much misinformation over credit and too little careful scholarship. Lawton's lack of attention to matters of real science and scholarship is a perfect example of the preoccupation with image rather than substance that continues to be all too common in this field.

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