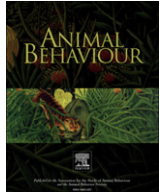


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Anniversary Essay

The enduring question of sex-biased dispersal: Paul J. Greenwood's (1980) seminal contribution

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In 1980, Paul J. Greenwood published a review of dispersal in birds and mammals that has been widely cited. The review evaluated possible explanations for sex-biased natal dispersal. It concluded that female-biased dispersal occurred in socially monogamous birds because males were using territorial resources to attract mates. In mammals, polygynous and polygynandrous males compete directly for and defend groups of females, and thus males more often disperse to find opportunities to sequester such groups. Thus, the primary difference between birds and mammals in sex-bias of dispersal appeared to be one of resource defence and mate defence mating systems. What made this review so seminal and what is the fate of his research question today? I begin with the excitement of the 'sociobiology' revolution and the fundamental nature and importance of the topic of dispersal. Furthermore, as all living things disperse, the topic of dispersal is central to many fields of study in behaviour, ecology, conservation and evolutionary biology. The hypotheses to explain dispersal that Greenwood reviewed (competition for resources, competition for mates and inbreeding avoidance) have been augmented, primarily by interest in lowered local kin competition as a fitness advantage for dispersers and kin cooperation as a reason not to disperse (*viz.* to remain philopatric in or near the natal area, particularly for female mammals). Current studies of Greenwood's question about sex biases in dispersal focus on testing the effects of local kin competition and on phylogenetic comparisons that reveal evidence of independent evolution of alternative dispersal patterns. © 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

GREENWOOD'S (1980) SEMINAL CONTRIBUTION

The most cited article from *Animal Behaviour* during the past 60 years is Paul J. Greenwood's (1980) review of dispersal patterns in birds and mammals (close to 2000 citations at this writing, more than twice that of the next closest contender). What is it about this review, the topic at the time that it was published and since, that makes it so popular and useful as a citation to so many studies? Sadly, we cannot get Paul Greenwood's impressions, since he tragically died in a house fire in 1988. To answer these questions, one can look back at the history of the field of animal behaviour, and the progression of ideas in behavioural science since this seminal work was written and published. This is a task of memory for me, since one of my early publications was a widely cited follow-up study in

Animal Behaviour (Dobson 1982). It is also necessary to look forward to understand how the questions in Greenwood's seminal work are still interesting and exciting today, for citations of his seminal review have steadily grown and continue to average about 100 per year.

We tend to think of some form of replication, either clonal division or sexual reproduction, as the essence of life. In part, we think of replication as the most basic aspect of living things because differential replication is a basic building block of evolutionary change by natural selection (Endler 1986). After all, Darwin's (1859) natural selection has proved the grandest of biological ideas. Nevertheless, there is something equally fundamental about dispersal: everything alive, from the smallest viruses and bacteria to the largest plants and animals, produce replicates that move away from their site of origin. Without movement away from the point of conception, new life cannot spread. All types of life have to move about to exist, and no species will long endure if individuals simply replace their parents in the parental location.

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During the late 1970s and early 1980s, behavioural ecologists were focused on basic questions about the evolution of behavioural traits, specifically, ‘what are the likely evolutionary advantages of particular behavioural or life cycle traits, given a particular environment?’ There was a search for grand ideas that would produce broad generalizations about fitness advantages of traits that were often shared by many species, like the dispersal patterns common within such broad taxa as classes of animals. The focus of advantage was often on energy savings or organismal growth, but also extended to the ‘stuff’ of natural selection, survival and ultimately reproduction. So Greenwood had a focus, ‘adaptive benefit’ and a fundamental question, ‘why should individuals leave a habitat where they know the ground, and venture into an unknown and perhaps dangerous realm?’

Seen in this context, Greenwood’s (1980; see also reviews by Greenwood & Harvey 1982; Greenwood 1983) review examined a fundamental process of all life. His focus on dispersal of birds and mammals is not surprising. We often study mammals, feeling some primitive kinship with them; birds are often subjects of study simply because they are so visible and colourful. In addition, due to the relative ease of permanently marking individuals, studies of birds and mammals allowed an important empirical breakthrough: the marking and tracking of individuals over their life spans. Given the sweep of biological diversity, however, birds and mammals are relatively small groups of organisms. But these are the groups in which enough study was available in the late 1970s for a review of dispersal to be timely. Lidicker (1975) had defined dispersal as movement away from a previous range into a completely new one, and the question of why organisms should take such leaps and bounds into an uncharted and unfamiliar world was becoming approachable. It is not easy to measure dispersal, since many individuals move far enough from their natal range to make measurement difficult. But, data were accumulating on birds and mammals. Researchers needed only articulation of an important question and insight about how to approach it. Paul Greenwood was clearly up to the task.

In the mid-1970s, E. O. Wilson (1975) had published his influential tome *Sociobiology*, and it introduced W. D. Hamilton’s (e.g. 1964, 1971) remarkable ideas about evolutionary thinking, from kin selection to living in groups, to an audience of young biologists. This was a time of great excitement among graduate students and their major professors alike (Paul Greenwood was then a student of Paul H. Harvey’s at the University of Sussex;

Fig. 1), in the subdiscipline of evolutionary biology that is now usually called behavioural ecology. So where did the idea of comparing birds and mammals come from? During a visit to Sussex by Craig Packer, Greenwood heard about male-biased dispersal in baboons (Packer 1975, 1979). From reading *Sociobiology*, Greenwood (1978) was impressed by the dispersal pattern of the pied flycatcher, *Ficedula hypoleuca*, in which more females apparently dispersed from the natal area (Berndt & Sternberg 1969). Thus, at least initially, the dispersal patterns of birds and mammals appeared different; but why should this be?

For Greenwood (1978), the task was two-fold. He needed to produce stronger evidence for the lesser studied of the two major taxa, the birds. For this he found two empirical gold mines: ringing records on caught and recaptured birds from the British Trust for Ornithology, and the amazing long-term data set on great tits, *Parus major*, at Wytham Wood, Oxford (since 1947, and in the care of Christopher M. Perrins). Faced with the intellectual challenge of explaining opposing patterns of sex-biased dispersal in birds and mammals, and armed with such outstanding empirical data, Paul Greenwood moved ahead on the empirical front by reviewing dispersal studies of both birds and mammals, and on the theoretical front to present ideas that might explain the difference between birds and mammals. These two tasks formed the core of Greenwood’s (1978) Ph.D. thesis. He divided movements into initial (natal dispersal) and subsequent (breeding dispersal) movements by males and females, although it appeared that in most species natal dispersal was most common.

Greenwood’s (1978) review was called ‘Mating systems, philopatry and dispersal in birds and mammals’. The presence of a diversity of mating arrangements in these two major taxa of terrestrial vertebrates, and Greenwood’s focus on both individuals that remain in the natal area and those that disperse, would prove a powerful combination. But Greenwood (1980) did something else common to evolutionary biology; he studied population-wide patterns that reflected underlying behaviours, rather than the behaviours themselves. This is quite common in behavioural ecology, particularly in life history theory, and complements the search for broad causal hypotheses to explain phenomena broadly among species. This was one of the powers of the sociobiology paradigm that is also common to ecological studies: broad categories and frequencies of phenomena are studied that allow us to generalize nature broadly, in order to gain an initial understanding. Later we learn that each species, at times even each population, has a unique pattern of traits and environmental circumstances.

Besides his focus on a fundamental aspect of biology and the attention that he drew to the stark differences in dispersal patterns between birds and mammals, Greenwood (1980) also cast a broader net by relating dispersal to fitness differences. The purpose of his review was the evaluation of evolutionary hypotheses to ‘explain’ sex-biases in dispersal patterns. Such hypotheses invoke potential fitness benefits that could have led to the evolution of the underlying complexes of behaviours that produce the species-typical patterns. Since social competition was a major focus of sociobiology, it was natural that competition would be invoked. Thus, competition for mates or resources (in this case used to attract mates) loomed large as general explanations for patterns of dispersal and philopatry. The ideas that competition for resources in general, relative to population size, and that aggression associated with local mate competition produced dispersal of socially subordinate individuals were also briefly evaluated. Another well-supported hypothesis from individual populations and species was that dispersal reduces the chance of inbreeding and associated fitness costs of inbreeding (viz. inbreeding depression). Nevertheless, both Greenwood (1980) and I (Dobson 1982) missed the potential importance of kin competition, perhaps confusing it with



Figure 1. Paul Greenwood (right) with Paul Harvey in their salad days (1976, photo by David J. Bousfield).

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