



## Why Ask "Why": The Importance of Evolutionary Biology in Wildlife Science

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*The Journal of Wildlife Management*, Vol. 55, No. 4. (Oct., 1991), pp. 760-766.

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*The Journal of Wildlife Management* is currently published by Alliance Communications Group.

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## WHY ASK "WHY": THE IMPORTANCE OF EVOLUTIONARY BIOLOGY IN WILDLIFE SCIENCE

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**Abstract:** The kinds of questions we ask in wildlife biology are at least as important as the methods we use to get answers to questions in research. In this essay, I urge wildlife biologists to vigorously pursue "why" questions rather than "how" questions or descriptive studies that should serve only as a starting point for our investigations. Behavioral ecologists are currently involved in a debate over explanations for biological phenomena called "levels of analysis": how many are there, what terms and definitions apply to each level, and the importance of clearly identifying which level an explanation emanates from given that there are correct explanations for the same phenomenon at each level. Asking "why" questions should lead the wildlife biologist into the realm of evolutionary biology and should place greater emphasis on understanding spatial and temporal variability in reproductive success and survival of wildlife species. I argue that our most useful insights about populations and communities should develop from long-term studies of this type.

*J. WILDL. MANAGE.* 55(4):760-766

In an earlier essay (Gavin 1989), I encouraged wildlife biologists to ask "why" questions, rather than to dwell strictly on descriptive relationships about wildlife and their habitats. My point is somewhat different from the other essays in this section, which emphasize the approach used to address research questions. They uniformly support the use of the hypothetico-deductive (H-D) method as recommended by Romesburg (1981). Nichols (1991) and Sinclair (1991) provide a particularly thorough review of many of the points made by Romesburg (1981). Although I strongly agree that we should aspire to the ideals of the H-D method, it would be redundant to reiterate a description of the meth-

od and supportive arguments already made by my colleagues.

My goal in this paper is to encourage greater emphasis in wildlife biology on the ultimate or evolutionary causes for the phenomena we observe in nature; by definition, this will force us to consider questions we have avoided in our research programs, possibly because we thought they were the sole responsibility of behavioral ecologists or evolutionary biologists who study basic biological problems. Ideally, it seems to me that if we understood *why* animals behave the way they do as individuals, then our understanding of dynamics at the level of the population would be more insightful. There is prob-

ably no short cut to developing this understanding, and this ideal will be impossible to attain in many circumstances due to a variety of logistical, financial, and methodological constraints. My belief is that basic research in wildlife biology is a necessity, not a luxury, and that wildlife researchers need to take responsibility for attempting to understand fundamental causes. I hope this essay will stimulate discussion among wildlife biologists and that it will generate introspection among those interested in prioritizing the questions we ask in our research programs.

The reasons a wildlife biologist does research are multifaceted, but this motivation probably involves a combination of (1) personal pleasure or satisfaction in understanding the natural world; (2) expectations on the part of the biologist's employer; (3) potential for professional advancement or enhancement (e.g., job security, money, or stature among peers), which may or may not be congruent with (2); (4) a commitment to provide information and insights that will improve the biological basis for managing wildlife; and (5) a desire to become a better "teacher" in the broadest sense of the word. The issue discussed here may be inconsequential with respect to (2) and (3), but I believe it should be positive with respect to (1) and essential to the ultimate success of (4) and (5).

There are no new data in this paper and probably no entirely new ideas. There is value, however, in repeating meritorious ideas already in the wildlife literature, in introducing recent ideas or debates current in other fields that are worth considering by wildlife biologists, and in trying to describe a perspective not now pervasive in our discipline. The continuous ebb and flow of ideas over time and space (i.e., disciplines) should encourage maturation of our science as we evaluate the merit of each idea. This is an appropriate sentiment on the 10th anniversary of Romesburg's (1981) paper, which I believe was offered in this same heuristic spirit. The approach we use to obtain answers *and* the kinds of questions for which we seek answers represent a necessary and sufficient combination that can be applied toward the goal of obtaining reliable knowledge.

Discussions with P. W. Sherman on the road to Idaho helped me formulate my ideas, and the paper benefitted from comments by E. K. Bollinger, S. A. Gauthreaux, Jr., B. May, T. D.

Nudds, R. T. Reynolds, P. W. Sherman, and an anonymous reviewer. This work was supported by the Department of Natural Resources, Cornell University.

## HOW AND WHY QUESTIONS

The fundamental categories into which research questions can be placed are usually identified as "how" questions and "why" questions. As Mayr (1961, 1982) pointed out, biology can be divided into 2 major divisions: functional biology and evolutionary biology. Functional biologists tend to be interested in *how* animals or plants do what they do, and they pursue the study of anatomy and physiology as 2 classical examples. "How" questions lead functional biologists to the *proximate cause* of some phenomenon. When a biologist asks *why* an organism has certain physical characteristics or behaves in a certain way, he or she begins tracing the pathway whereby this organism acquired such traits and the effects such traits (i.e., adaptations) have on the reproductive success of the organism. This is the realm of evolutionary biology and *ultimate causation*. Mayr did not imply that 1 approach was superior to the other; he merely pointed out that each major division of biology deals with a different level of explanation of biological cause and effect. Both levels are needed for a complete understanding of any biological phenomenon (Pianka 1988).

Tinbergen (1963) provided an expanded discussion of these ideas that included 4 levels of biological inquiry, rather than 2. He divided functional biology ("how" questions) into investigations of individual ontogeny (i.e., effects of age and experience) and physiological mechanisms. Evolutionary biology ("why" questions) was divided into evolutionary origins and functional consequences (i.e., current adaptive value). This schema has manifested itself more recently in a paper by Sherman (1988), which precipitated a debate over what biologists call "levels of analysis" in behavioral ecology (Jamieson 1989, Sherman 1989, Armstrong 1991, Emlen et al. 1991, Jamieson 1991). Such debates are not unique to behavioral ecology. The critique by Matter and Mannan (1989) of Romesburg's (1981) analysis of the threshold-of-security hypothesis seems to result because each is focused on a different level of analysis. Matter and Mannan (1989) suggested the testing of a particular proximate mechanism (i.e., behavioral spacing) that might explain the threshold-

of-security, but Romesburg (1981) was more interested in the form of the relationship between fall-to-spring population size, rather than the mechanism that produced the relationship. Romesburg (1989:1179) recognized the qualitative difference between these arguments when he said that Matter and Mannan's "... hypothesis would not satisfy someone wanting an explanation at another level. ..." Sherman's (1988) point is that biologists working at different levels of biological inquiry (or levels of analysis) must recognize these levels to avoid fruitless arguments about whose explanation of a biological phenomenon is correct. They may each be correct given the level of investigation at which they are working.

This may all seem to academic for applied biologists, but there are 2 distinct lessons to appreciate: (1) there are different levels (probably 4) at which questions can be asked about biological phenomena, each with answers that are correct *within* that level—alternative explanations for phenomena legitimately compete only with others at the same level of analysis; and (2) the problems we want to understand as wildlife biologists are asked within one of these levels, whether we know it or not. I believe wildlife biologists can benefit from knowledge of this discussion among other biologists, and that this may lead to a more conscious evaluation of the kinds of questions we ask and the way we frame those questions.

## AN EXAMPLE

Many species of north temperate birds migrate between northern breeding areas and southern wintering areas and exhibit breeding site fidelity. One might ask how a warbler finds its way from Europe to Africa and back again the following year. This general question has fueled an active experimental research program among certain European and American ornithologists who have investigated migration in numerous species for about 2 decades. This research has generated testable hypotheses about the proximate mechanisms involved in bird migration, and this group of scientists has employed the H-D method rigorously. Celestial, magnetic, visual, acoustic, and olfactory cues, singly or in combination, appear to aid many birds in their orientation and navigation from 1 place to another (reviewed in Able 1980, Gwinner 1990). Some species (perhaps many) can even correct their orientation after being

displaced by prevailing winds (e.g., Moore 1990). This suite of abilities helps explain what mechanisms birds use to find their way across long distances (level = physiological mechanisms). The mechanisms birds use to find their wintering areas during their first autumn are probably different from that used by older birds (Able 1980), indicating that young birds probably learn how to get there and back during their first migration (level = ontogenetic processes).

But *why* do migratory birds return regularly to the same field or patch of forest to breed? There are numerous hypotheses for explaining the origin of migratory behavior (Gauthreaux 1982, Cox 1985), which include the waxing and waning of glacial periods, the flush of plant and animal productivity in the spring at high latitudes, and movement to avoid interspecific competition, to name a few (level = evolutionary origins). An answer at another level would seem to be that reproductive success and/or survival of individual birds that migrated was higher than conspecific individuals that did not migrate in a fairly precise manner (level = functional consequences). The historical events that contributed to the evolutionary origin of site fidelity may no longer exert the same selective pressure that they once did, but the behavior persists because its benefits with respect to reproductive success exceed the costs, on average, over time.

## A PERSONAL ANECDOTE

Since 1981, with the help of many technicians, I have studied the population biology of bobolinks (*Dolichonyx oryzivorus*) in upstate New York. Bobolinks are icterines that nest in grassy fields in the northern United States and southern Canada and winter in South America. Bobolinks exhibit breeding site fidelity. Individuals often return to the same area of a hayfield where they nested in previous years, after migrating from the pampas of Argentina and back again 7–8 months later, an annual round trip of about 20,000 km. One female marked as an adult in 1982 returned again in 1990; the inference is that she made this migration at least 9 times during her life. If so, the distance she flew in migration alone (i.e., 180,000 km) is equal to 4.5 trips around the earth at the equator! Something is known about "how" bobolinks accomplish this incredible feat. Beason and Nichols (1984) showed experimentally that bobolinks were able to orient appropriately to magnetic fields, and that bobolinks contained deposits of

iron oxide (probably magnetite) in their heads (i.e., mechanism).

Our early studies indicated that 25–50% of the breeding adults returned to the same field the following year to breed, with some variability in return rates among years and among sites. We were interested in the functional consequences of site fidelity, or "why" some bobolinks returned to the same breeding site the following year and others did not. There are 2 general answers to this question: (1) there was some choice or "decision" by each individual to return or not, or (2) those individuals that did not return simply had died. Examining the relationship between reproductive success in year  $t$  and the probability of that individual returning in year  $t + 1$ , we found that adults that fledged young 1 year were more likely to return to that site the following year than adults that fledged no young. Limited mist-netting at other sites in the vicinity of our intensive study sites resulted in the capture of 5 of our former residents, so we knew that not all individuals that failed to return to the same site had died. (Only 2 of these former residents were known to produce fledglings at their previous site, and all 5 individuals moved to sites of higher bobolink density.) We concluded that bobolink adults were making some kind of experience-based choice to return to their former breeding site based on their reproductive success at that site, and we published the results based on data collected at Bald Hill and Shackelton Point, which are 95 km apart, in upstate New York (Gavin and Bollinger 1988).

Toward the end of this phase of our work, Eric Bollinger, then a graduate student, began studying bobolinks at Moore Road, a hayfield about 4 km from Shackelton Point. His results on breeding site fidelity were somewhat different. At Bald Hill and Shackelton Point, where the results were nearly identical, 25% of the females and 44% of the males resident 1 year returned the following year. At Moore Road, 49% of the females and 70% of the males returned. Surprisingly, in view of our hypothesis, even adults that had been unsuccessful at fledging young the previous year tended to return to Moore Road. This population was more dense and produced more fledglings per ha than those at Bald Hill and Shackelton Point (i.e., 9.4 fledglings/ha vs. 1.5 fledglings/ha), and more fledglings were produced per adult at Moore Road than at the other 2 sites. Based on these results,

we broadened our hypothesis: individuals seemed to respond to their own reproductive success at the 2 low-quality sites, but once they became established at the high-quality site (quality defined by the No. fledglings produced/unit of area and not nest success), they responded positively to the generally high level of fledging success in that field (Bollinger and Gavin 1989).

A dilemma that field biologists often face is whether to conduct an experiment to test a hypothesis, given that the experiment itself would disrupt other phenomena under study in the same population (e.g., Grant and Grant 1989). Because of the a priori way in which he treated his hypotheses, Bollinger (1988) saw an opportunity to use hay-cropping as a random mortality event to destroy a sample of nests at Moore Road and at a small auxiliary site in 1985. In effect, hay-cropping was a fortunate (for us) experimental treatment. As expected, adults that had no successful nests because of hay-cropping, even though they were not harmed, returned less frequently than adults that fledged young (Bollinger and Gavin 1989). In addition, Haas (1990), another graduate student of mine, removed eggs or nestlings from a random sample of nests of American robins (*Turdus migratorius*) and brown thrashers (*Toxostoma rufum*) in North Dakota to test the mortality and choice hypotheses. The return rate of adults of both species was significantly higher for adults with nests that fledged young than for adults that did not, regardless of whether nest failure was natural or experimentally induced. These experiments on 3 species of passerines allow us to confidently reject the null hypothesis that selection of breeding habitat is not influenced by previous experience.

#### IMPLICATIONS (VALUE) OF ASKING WHY

Perhaps the most important impression we have developed in this work is that all birds are not equal. Although individuals that fledged young returned at a significantly higher rate than unsuccessful individuals, some adults that fledged young from their territory did not return, and some that returned had not fledged young the previous year. One possible reason for the lack of perfect precision between fledging young and return behavior is that we have not yet identified the exact element of reproductive success the birds use as a memory cue

about the suitability of a previous breeding site. During our studies, we documented that bobolinks participate in extra-pair copulations that result in males siring young in nests belonging to females on other male's territories (Gavin and Bollinger 1985, Bollinger and Gavin 1991). Males may be using the number of copulations they obtain or the number of different females with which they copulate at a site as their criterion for returning to that site the following year. We do not know how these behaviors would be correlated with fledging success on a particular male's territory, which was our independent variable. Continuing to ask "why" moves us slowly through successive layers of complexity toward a reliable explanation of breeding site fidelity.

The dynamics described here are due to the behavior of individuals grouped into what we usually call populations. This behavior appears to be driven primarily by their attempt to increase reproductive success or avoid low reproductive success which, along with survival, constitute the main ingredients on which natural selection acts and affects evolutionary change. This is not just some abstract theoretical idea; it has relevance to the need to understand why individuals behave as they do, so that populations can be managed. Bobolinks select breeding habitat in early May based on past experience at that site and the "appearance" of the vegetation, not knowing that this field may be mowed at the peak of nesting 5–6 weeks later. These individuals behave this way as a result of selection over many generations.

Ironically, some of the fields with high quality vegetation (for hay production) in early May when the birds settle were fields managed by full-time farmers; these farmers renovate fields by reseeding or fertilizing when the vegetation becomes less productive. These farmers tend to cut early, which eliminates all nests and results in zero reproductive success for all individuals in the field (Bollinger 1988). In contrast, part-time farmers, who usually have other full-time jobs, work fields longer before they reseed or fertilize; this results in habitat preferred by bobolinks in upstate New York relative to fields that are renovated more regularly. Part-time farmers usually cut their fields later in the summer after the birds have completed nesting. As a result, the majority of bobolinks and other grassland birds in upstate New York are probably

produced in low quality hayfields, even though many birds attempt to nest in fields with high quality vegetation.

Our conclusion for management of bobolinks and other grassland birds with similar requirements is to mimic the practices of part-time farmers. It is better to renovate fields less often and to mow later than an efficient farming operation might dictate. (We have also observed that female bobolinks seem to prefer nesting in fields where the vegetation has been cut and removed rather than simply cut.) Habitat choice coupled with breeding site fidelity apparently results in some fields that produce many fledglings relative to other fields in the same area; protection of a site like Moore Road would result in as many young being produced as protecting 6 times as much acreage that is the quality of Bald Hill or Shackleton Point. Results of Breeding Bird Surveys, which provide an index to the relative number of males detected along predetermined routes, may not be correlated with productivity at all. These surveys probably provide an index to male selection of breeding habitat only, and thus serve as an indicator of potential habitat for bobolink production.

Evolutionary theory tells us that individuals that maximize lifetime reproductive success are selected. The morphological, physiological, and behavioral traits exhibited by individual organisms probably contribute to their ultimate reproductive success; by definition, these are adaptations. Habitat selection, for example, is a behavioral trait that wildlife biologists have emphasized in their studies, because of the obvious importance of habitat to wildlife and because habitat is something we can potentially improve or protect (Gavin 1989). But animals probably select habitat for breeding based on cues correlated with future successful reproduction that have worked over evolutionary time. For example, Northern lapwings (*Vanellus vanellus*) select meadows that are grey-brown rather than green, because the former are poor meadows where the grass will remain low, and they represent habitat to which this species is adapted (Klomp 1953, cited in Hilden 1965). When those cues become uncoupled from the reproductive success historically associated with them because of human influences, the cost/benefit algorithm inherent in each individual may not lead to high reproductive success because of evolutionarily novel events caused by human

disturbance. That is, animals have been selected to respond to cues in such a way that these responses lead to increased survival and successful reproduction over time. The problem now is that the natural world and the dynamics of its elements have been changed by humans (dramatically in many cases, subtly in others) over a relatively short time. The cues may be there, but the consequences of responding to those cues may now be different. An evolutionary biology perspective may help us understand this dilemma.

In the case of migratory birds, individuals probably choose breeding habitat in the spring based on their previous reproductive success and physical cues (e.g., structure of vegetation, plant phenology, insect abundance) provided by that habitat. However, human land-use practices can change the rules of the game. As wildlife biologists, we have focused on the proximate relationship between wildlife and habitat by describing those habitats that individuals use. Without knowing the reproductive success of individuals in these habitats, it is difficult to recommend how much of which habitats to protect, or how to change practices (e.g., selective logging) that currently result in reduced reproductive success in that habitat, but which have not yet affected the organism's choice of habitat. We have used habitat choice by organisms as our surrogate for what really counts in the dynamics of populations—survival and reproductive success (Van Horne 1983, Murphy and Noon 1991). In a pristine world, this surrogate probably had a high correlation with survival and reproductive success, but we can no longer assume this to be true.

Do these conclusions apply only to migratory birds? Probably not. Young individuals of most species disperse from their natal area during their first year (Greenwood 1980). Presumably they search for a breeding site that has a suitable physical and social environment. These individuals must be using cues gathered from the environment, which have been associated historically with reproductive success. It would be interesting to compile a list of examples where the cues animals use in selecting breeding habitat seem to be "wrong" given the current dynamics of the environment. The current relationship between wood ducks (*Aix sponsa*) and their choice of nest boxes, which I highlighted earlier (Gavin 1989), could begin the list.

## CONCLUSIONS

The major thesis of this essay is that asking "why" questions should lead us closer to understanding why organisms respond the way they do. Specifically, it is important to know reproductive success in the various habitats used by the organisms we wish to manage. Asking what habitat type species  $x$  prefers is neither a "how" nor a "why" question. Obviously, it is the correct starting point for many studies, but it is only a beginning and only descriptive. We should really be interested in developing insights about the structure and function of populations and communities, and this requires studies to be of long duration. Regardless of whether "how" or "why" questions are asked, development of insights requires use of a rigorous methodology; a combination of retrodution and the H-D method are probably most appropriate for wildlife science (Romesburg 1981). It is my contention, however, that answers to "why" questions are more likely to be of value in wildlife management than answers to "how" questions.

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Received 23 April 1991.

Accepted 2 July 1991.

Associate Editor: Morrison.