In My Opinion: Hypotheses in wildlife science

Fred S. Guthery, Jeffrey J. Lusk, and Markus J. Peterson

Abstract The hypothesis is a core element of science. However, the concept is multifaceted; we address the need to understand the full range of perspectives toward "hypothesis" so that the concept may be applied most usefully in wildlife science. "Hypothesis" has multiple meanings ranging from any speculative thought, to imaginary entities that explain phenomena, to concrete, specific conjectures on the process(es) that lead to an outcome. The latter conjectures are called working or research hypotheses and are the backbone of hypothetico-deductive science. More than conjectures on the existence of a pattern ("existential hypotheses"; e.g., latitudinal effects on clutch size), research hypotheses are conjectures on why the pattern exists. The research hypothesis has gone from nearly nonexistent in the wildlife research literature of the 1970s and 1980s to a prevalence of about 25% in the 1990s and 2000s. We provide several examples of research hypotheses and deductions derived therefrom as formulated by members of the wildlife research community. Although we advocate the use of research hypotheses, we also argue that studies of management treatment effects (magnitude of effect germane, research hypothesis passé) and simple descriptive studies (research hypothesis unnecessary) still have an important place in wildlife science.

Key words existential hypothesis, hypothesis, null hypothesis, research hypothesis, science, wildlife science, working hypothesis

Scientists widely regard hypotheses as a key element of science; indeed, most would say hypotheses are central. Because the word "hypothesis" has multiple meanings and nuances, however, it often is unclear to what they are referring. Are there alternative types of hypotheses, some of which serve science better than others? How should one deal with a hypothesis after generating one? Is it mandatory to invoke hypotheses of one sort or another in science, or is it possible to do "good science" in the absence of hypotheses?

We address the above questions relative to wildlife science. We begin by discussing alternative meanings of "hypothesis," including those from general discourse as well as those from the more specialized realm of science; we distinguish between a hypothesis and a theory. From the set of definitions, we select what are known as working (Chamberlin 1890) or research hypotheses (Romesburg 1981) for further development. Such hypotheses are the principal intellectual instrument of the scientist (Beveridge 1957), the argument that binds diverse research to theme (Sinclair 1991), and the backbone of hypothetico-deductive experimentation (Romesburg 1981). We do not take it as our purpose to explain the importance of hypotheses to wildlife science because this subject has been treated in detail elsewhere (e.g., Romesburg 1981). We provide a broad-based set of examples and show how wildlife scientists have used research hypotheses and deductions therefrom to advance knowledge. We maintain that genuine research hypotheses remain underused in wildlife science (Romesburg 1981, Guthery et al.

2001*b*), and we hope this exposé will assist in correcting this situation. Finally, we identify research that is important to wildlife science and management but that need not be driven by any form of hypothesis.

Meanings of "hypothesis"

We begin with 2 meanings of "hypothesis" commonly used in general discourse and adopted by science. Hypothesis may be defined as 1) the antecedent of an if-then statement, or 2) a guess, conjecture, supposition, surmise, or speculation (or, loosely, a theory; see below). Wildlife scientists clearly perceive the first half of an if-then statement to be a hypothesis. The second meaning appears in the wildlife literature in a number of ways, perhaps most frequently in the form of statistical hypotheses. Ashmole's hypothesis provides another example. It is simply a conjecture that within a bird species, clutch size is larger in northern than in southern latitudes. Another example is the hypothesis, or conjecture, that birds forage more efficiently in flocks than as individuals (Hilborn and Mangel 1997). Thus, in a most general sense, a hypothesis can be viewed as any speculative thought. This definition would include alternative statistical or mathematical models posited to explain or describe phenomena (Guthery et al. 2001*b*, Burnham and Anderson 2002). Although Hilborn and Mangel (1997) argued that mathematical models were not hypotheses, they certainly are under this general definition.

A theory, in contrast to a hypothesis, has accrued consistent and considerable experimental support. That is, a theory is a hypothesis that has stood up to rigorous experimentation without being rejected. Scientists are more certain of theories than of hypotheses but not to the point that they see theories as immutable laws of nature. Darwin's theory of evolution by natural selection is an example of such a theory. Therefore, what differentiates a hypothesis from a theory from a natural law is the degree to which it has successfully withstood scrutiny and challenge. Few theories in wildlife science and ecology rise to the stature of natural law because definitive experimentation is often impractical, if not impossible. For example, natural selection as a mechanism of evolution has been and continues to be the focus of intense experimentation. However, because the average lifespan of a human being, and even of civilization, is trivial in comparison with evolutionary timeframes, it is unlikely humanity will ever witness a speciation event among vertebrates.

Scientists have long held that a hypothesis can be an assumption, something taken as true, or something imagined for the sake of argument or explanation. Poincaré (1952) devoted a book to this form of hypothesis, which Romesburg (1991) called an isolate and Feynman (1998) called a construct. Such hypotheses represent contrivances of the human mind, such as the threshold of security—which explains similar breeding densities of game birds among years (Errington 1945), the niche as an *n*-dimensional hypervolume (Hutchinson 1957)—which provides a construct for understanding partitioning of resources among sympatric organisms, or slack in configuration of habitat patches (Guthery 1999)—which explains why configurations with different properties are of equal value to animal populations. This form of hypothesis is quite abstract and rare in wildlife science.

More commonly, wildlife scientists consider a hypothesis to be a tentative, universal explanation for an observed ecological event or a pattern (Krebs 2000)—the cause(s) of the event or pattern or the processes that led to the event or pattern. This defines a working (Chamberlin 1890) or a research hypothesis (Romesburg 1981).

Examples of research hypotheses

Before proceeding with examples of research hypotheses, we distinguish what we shall call existential hypotheses from research hypothesis. The null hypothesis, Ashmole's hypothesis, and the hypothesis that birds forage more efficiently in flocks than as individuals (see above) are existential because they imply the existence of a pattern. Conversely, a research hypothesis is a conjecture on why the pattern exists. With regard to Ashmole's hypothesis, for example, we might conjecture (research hypothesis) that pre-incubation storage times are longer in northern (cooler) latitudes than in southern (warmer) latitudes in the northern hemisphere. Longer storage times might permit more eggs to be laid before the adult had to regulate egg temperature to protect embryos from hyperthermia or to prevent staggered hatches, thus explaining larger clutches in northern as compared to southern latitudes.

From a human-interest standpoint, our first example of a research hypothesis comes from the work of Dr. Martha McClintock, as reviewed by Clark and Grunstein (2000). McClintock sought to explain why the menstrual cycles of women (especially friends) living in close proximity became synchronous. She and other researchers considered a number of hypotheses that might account for this observation, and she finally focused on human pheromones as an explanation. Research results with synchronous estrus cycles in rats (*Rattus* sp.) were supportive. Eventually McClintock demonstrated that axillary secretions (the site of pheromone production in humans) of one woman could alter the cycle of another.

Further examples of research hypotheses come from the pages of the wildlife science literature. Vaughan and Keith (1981) tested the hypothesis that winter food shortage initiated cyclic declines in snowshoe hare (*Lepus americanus*) numbers in Alberta. McCorquodale (1991) tested the hypothesis that the unexpected success of elk (*Cervus elaphus*) in the arid shrub–steppe of Washington could be explained because effects of low primary production in the shrub-steppe were offset by high availability of foraging areas and low intercommunity variation in forage production. Hernández et al. (2003) evaluated the limited-bunchgrass versus the nest-protection hypotheses to explain a high prevalence of northern bobwhite (*Colinus virginianus*) nests in patches of prickly pear cactus (*Opuntia* spp.) in the Rolling Plains of Texas.

Attempts to understand boom–bust fluctuations in populations of New World quails living in semiarid environments illustrate how research hypotheses may evolve through time. The basic question that directed research beginning in the 1940s was, "What causes the rather violent year-to-year fluctuations in productivity and populations of these birds?" This question led to a series of research hypotheses that were tested in laboratory, field, or both.

Nestler's (1946) work on vitamin A nutrition of bobwhites generated the first known research hypothesis on the cause of boom-bust behavior. Nestler demonstrated with penned birds that increased concentrations of vitamin A in the diet (starting at 0 IU/unit mass) were associated with asymptotic increases in egg production, egg hatchability, and survival of chicks and breeding birds. As a result of Nestler's (1946) study, biologists advanced the hypothesis that variation in vitamin A nutrition was the cause of boom–bust fluctuations in the field. Here we have a genuine research hypothesis, a conjecture on process involving a one-link cause–effect chain.

Two field tests of the vitamin A hypothesis were conducted. Lehmann's (1953) results with northern bobwhites in southern Texas did not support the hypothesis. Hungerford's (1964:141) study of Gambel's quail (*Callipepla gambelii*) indicated "Vitamin A or a closely associated substance derived from green plant material apparently acts as a stimulator which influences the rate of laying...."

Due to contradictory results or Hungerford's (1964) ambiguity ("closely associated substance"), wildlife scientists had little evidence to refute or support the vitamin A hypotheses and, not surprisingly, were dissatisfied with it. They still seemed, however, convinced that the cause of boom–bust behavior entered through the beak. This assumption led to the formulation and testing of a set of diet–nutrition hypotheses.

Observing that consumption of phytoestrogens inhibited the production of sheep in Australia (Leopold 1977), Leopold et al. (1976) developed the research hypothesis that concentrations of phytoestrogens were higher in green plants (a component of the quail diet) during drought years than during rainy years. Field results were supportive. If these steroids inhibited reproduction performance of quails, then an explanation of boom–bust behavior was at hand. Unreplicated testing with 3 pairs of California quail (*C. californicus*) on 3 different diets, 1 containing high levels of phytoestrogens, suggested that plant hormones inhibited production. Subsequent research debunked the phytoestrogen hypothesis; while these steroids inhibit production in quails, it is not possible for wild birds to consume the quantities necessary for such inhibition to occur (Cain et al. 1987).

Still seeking an oral pathway for the boom-bust phenomenon, Cain et al. (1982) evaluated variation in phosphorus nutrition (the research hypothesis) as causally related boom–bust population dynamics. They concluded such variation could contribute to, but could not fully explain, annual variation in productivity.

Although we cannot know the thinking of research biologists after the above-cited studies appeared in print, we assume they were becoming more circumspect about the role of nutrients in population dynamics and more general in their search for understanding of the boom–bust process. Accordingly, more comprehensive hypotheses appeared for experimental challenge.

One of the first involved a hormone-mediated, nonspecific stress response (Cain and Lien 1985). The research hypothesis was that a nonspecific stress response inhibited chick production in drought years, whereas lack of the response permitted normal production in rainy years. Cain and Lien (1985) demonstrated in the laboratory that the administration of corticosterones (stress hormones) to captive birds resulted in reproductive dysfunction and that water stress could elicit increased levels of corticosterone.

Cain and Lien (1985) demonstrated the feasibility of the stress response as a mediator of reproduction, but the operative stressor(s) remained in question. An obvious stressor to test based on their results was substandard water intake. Accordingly, Guthery and Koerth (1992) tested the research hypothesis that substandard water intake contributed to reproductive failure of bobwhites during drought, whereas water nutrition was not an issue during rainy years. They deduced that under this hypothesis, preformed water available in forbs during drought would be demonstrably insufficient for population needs. This reasoning demonstrates that one way to challenge a research hypothesis is to determine whether conditions exist (e.g., deficiency of preformed water) that permit a conjectured process (e.g., stress inhibition of production) to operate. They also predicted that provision of surface water would reverse the effects of drought on bobwhite production. Neither the conjecture on the insufficiency of preformed water during drought nor the prediction of stabilized production with water supplementation held in a field experiment. Thus, the research hypothesis on substandard water intake was rejected.

Yet the Cain and Lien (1985) findings on stress hormones remained tantalizing. Accordingly, Harveson (1995) developed a macronutrition-stress hormone hypothesis to explain reproductive failure during drought. He conjectured that increasing day length in spring awakens a breeding urge, as governed by hormones. He further conjectured that during drought years, with possibly low availability of dietary proteins, fats, and carbohydrates, substandard macronutrition contradicted the breeding urge, thus leading to nonspecific stress, the release of corticosterones, and reproductive quiescence. This hypothesis was rejected because field study indicated breeding bobwhites carried, on average, higher levels of stress hormones than nonbreeding individuals (the data were contrary to expectation).

As scientists labored to find a nutritional explanation of boom–bust behavior (while belaboring the assumption that nutrition mediated the behavior), other data were accumulating on correlates of reproductive performance in New World quails. Biologists had long known that hot summers were associated with substandard reproductive performance in quails (Leopold 1933:297, Robinson and Baker 1955, Stanford 1972, Klimstra and Roseberry 1975). Guthery (1997) formulated the heat hypothesis as a nonnutritional explanation of boom–bust behavior. The hypothesis stated that annual variation in heat loads near the ground explains a large percentage of the variation in annual production. Heat would act to suppress intensity (percentage breeding) and duration of breeding seasons. Field research in southern latitudes indicated thermal intensity during the breeding season is sufficient to cause broad-scale suppression of quail reproduction in time and space (Guthery et al. 2001*a*). The heat hypothesis, however, remains provisional and wildlife science continues to lack a clear understanding of the causes of booms and busts.

Let us reflect momentarily on the boom–bust odyssey. A gifted scientist might have single-handedly generated all of the competing hypotheses described above and, thus, fallen in line with Chamberlin's (1890) advocacy of multiple working hypotheses, which he believed would protect the scientist from becoming too enamored, and biased in favor, of any one hypothesis. However desirable multiple hypotheses may be, science seldom works in a competing-hypothesis mode (Beveridge 1957). Rather, scientists develop and test sequences of hypotheses, as was done in the attempt to understand boom–bust dynamics in quails. The progression of knowledge and the need of fodder for thought undoubtedly guarantee that such sequences are present in the execution of wildlife science.

Deducing from research hypotheses

As the above examples illustrate, a genuine research hypothesis implies a testable, conceptual model of a cause–effect process. Testability implies falsifiability, which is a criterion that separates scientific from nonscientific hypotheses (Popper 1959). Given a process, it is possible to deduce events that will occur if the process holds (to make predictions in a hypothetico-deductive sense; Romesburg 1981). Predicting what is expected to occur if the hypothesis holds typically is necessary in ecological research; it often is impossible to test the hypothesis *per se* because of issues of cost and scale. Rather, it is only possible to test deductions under the hypothesis.

Rave and Baldassare (1991) provide a good example of hypothetico-deductive science in a field setting. They tested competing hypotheses (temperature effects, diet) explaining lipid dynamics in wintering green-winged teal (*Anas crecca*). They deduced that if mass of lipid reserves varied inversely with winter severity, then the temperature hypothesis was supported. Conversely, if carcass composition varied more with food composition than winter severity, then the diet hypothesis was supported.

Another good example appears in Barten et al. (2001:78). These authors used a blend of existential hypotheses (as we defined them) to ascertain whether and to what degree forage acquisition and predation risk (competing research hypotheses) governed the field behavior of female caribou (*Rangifer tarandus*). Under the forage-acquisition hypothesis they deduced, among other predictions, that "forage abundance and quality would be greater at sites used by females with young than at sites used by females without young." Under the predation-risk hypothesis, they deduced, among other predictions, that "forage abundance and quality would be lower at sites used by females with young than at sites used by females without young." All of these predictions are testable in the practical as well as theoretical senses.

Although a research hypothesis does not preclude banal predictions, the predictions of Rave and Baldassarre (1991) and Barten et al. (2001) were substantive with respect to processes in nature. Conversely, predictions derived from a statistical hypothesis (null or alternative) usually are pedestrian.

Subsequent to Romesburg's (1981) appeal for applying research hypotheses in a hypothetico-deductive milieu, what might be called camouflaged statistical hypotheses began to proliferate in the wildlife literature. Some authors in *The Journal of Wildlife Management* and *Wildlife Society Bulletin* predicted the direction (<, >) of an effect. Others formulated more complex hypotheses, such as, "We tested the hypothesis that habitat characteristics differed among summer communal, winter communal, summer solitary, and winter solitary roosts." These statements could be viewed as camouflaged alternative hypotheses that imply null hypotheses; they are not, in our estimation, true research hypotheses (we do not imply the authors took them as such). Cherry (1998) and Johnson (1999) argued that the application of inferential statistics was inappropriate in such situations because researches knew a priori that—assuming they had sufficient sample size—habitat characteristics would indeed differ among summer communal, winter communal, summer solitary, and winter solitary roosts. The question actually was the degree to which they would differ.

Occurrences of camouflaged statistical hypotheses in the wildlife literature could reflect 2 circumstances. First, some scientists consider the alternative statistical hypothesis to be a synonym for research hypothesis (Johnson 1999). This could be true in a most primitive sense that verges on being nonscientific. However, contrast the typical, rather pedestrian alternative and null hypotheses with the thoughtful deliberations on process made by Rave and Baldassare (1991) and Barten et al. (2001); such deliberations are an essence of science, and the alternative statistical hypothesis is vacuous in comparison. Second, camouflaged statistical hypotheses could reflect studies wherein hypotheses were unnecessary or only obliquely relevant, and the authors simply were responding to social imperatives from the community of editors and referees in formulating any hypothesis at all.

Hypothesis-free science

While hypothesis-free science might sound like an oxymoron to the well enculturated wildlife scientist, we envisage 2 situations where legitimate wildlife research can be conducted in the absence of research hypotheses. The first involves research where outcomes are not necessarily in question, only the magnitude of the effect. As Edwards (1992:2) observed, "in almost all situations we know that the *effect* whose significance we are measuring is perfectly real, however small; what is at issue is its magnitude" (emphasis in original). Similarly, Cherry (1998), Johnson (1999), and Anderson et al. (2000) maintained that estimating the magnitude of effects often is of fundamental importance to wildlife scientists.

Studies on the effects of management treatments (e.g., predator control, approaches to grazing, increased food supplies, water development, prescribed burning) might, in general, be best viewed under a magnitude-of-effects perspective (absolute or relative increases or decreases in response variables) rather than a hypothetico-deductive or statistical perspective. Here the research hypothesis, often quite mundane, is contained in the treatment. Moreover, managers are unlikely to execute such treatments if null or negative effects were expected. In many cases, such as prescribed burning or removing all livestock from a heavily grazed system, there remains no doubt that effects on biotic communities will occur; at question is only the precise nature and magnitude of the response. Why encumber the results of such studies with other than simple, descriptive statements regarding the magnitude of effect? Such statements provide concise and meaningful information to managers.

The second situation where hypotheses seem unnecessary is the simple descriptive study. This type of study is necessary (Herman 2002) and common in wildlife science; it may be identified with justifications that contain phrasing such as, "there is little information on this topic," or "we were the first to measure." Additionally, most studies done under information-theoretic protocols (Burnham and Anderson 2002) are simple descriptive because they rarely, if ever, are associated with deductions derived from genuine research hypotheses. More commonly, the a priori models are based, at least in part, on the data available for analysis within a set of existing ideas on how nature might operate. In many ways, the numerous models typically compared using information-theoretic protocols are much more analogous to statistical than research hypotheses (Guthery et al. 2001*b*). The information-theoretic approach would seem to be an especially powerful method of testing existential hypotheses.

Simple descriptive studies remain justified, in our view, from at least 2 perspectives. First, when a new idea or technology (e.g., radiotelemetry, geographic information systems) appears, research on the idea or using the technology is perforce descriptive at the outset. There are few or no events or patterns upon which to hypothesize. Second, a population of simple descriptive studies that addresses the same general topic may reveal patterns that could not be observed in the absence of such studies. Ashmole's (existential) hypothesis on latitudinal trends in clutch size, for example, could not have been formulated without descriptive data on clutch size. Similarly, information-theoretic approaches can be particularly effective at determining whether the magnitude of a difference is sufficient to warrant inclusion in descriptive models (Anderson et al. 2000, Burnham and Anderson 2002). Moreover, these approaches typically utilize simple descriptive data.

Concluding remarks

The word "hypothesis" has multiple meanings in human discourse, including that of scientists. Those meanings range from any speculative thought to imaginary contrivances of the mind to concrete, specific conjectures on the process(es) that lead to an outcome. Romesburg (1981) believed that wildlife science was deficient in those concrete, specific conjectures (research hypotheses) and deductions derived therefrom; we hope this exposé will benefit the wildlife research community by providing examples of research hypotheses and associated deductions as applied by members of the community itself.

Romesburg's (1981) paper appears to have been influential in bringing the research hypothesis to the fore in wildlife science. We conducted an informal survey of all papers that appeared in volumes 35 (1971, $n = 124$), 45 (1981, $n = 162$), 55 (1991, $n = 104$), and 65 (2001, $n = 105$) of *The Journal of Wildlife Management* to determine the prevalence of research hypotheses. We censored studies of methods, management treatment effects, and philosophy (including reviews) in analyzing trends in application of research hypotheses. That decision excluded 40.3% of papers in volume 35, 48.8% in volume 45, 53.8% in volume 55, and 56.2% in volume 65. The percentage of remaining papers that contained explicitly stated research hypotheses was 0.0% for volume 35, 2.4% for volume 45, 25.0% for volume 55, and 25.8% for volume 65. Thus, prior to Romesburg's (1981) paper, the research hypothesis was rare in *The Journal of Wildlife Management.* Ten and 20 years after his paper, however, the research hypothesis appeared in about 25% of papers that potentially could have been based on such hypotheses. This increase is encouraging for wildlife science. We maintain that some of the remaining 75% would have benefited from the inclusion of explicit research hypotheses.

While we advocate increased use of true research hypotheses in wildlife science, we also argue that there should still be a place in basic and applied ecology journals for studies that are not driven by explicit research hypotheses and which use no trendy analysis technique. For example, research quantifying the magnitude of treatment effects is critical to wildlife science. Similarly, as Romesburg (1981) argued, simple descriptive studies provide the grist for the hypothetico-deductive mill—we cannot form meaningful research hypotheses in a data-free environment.

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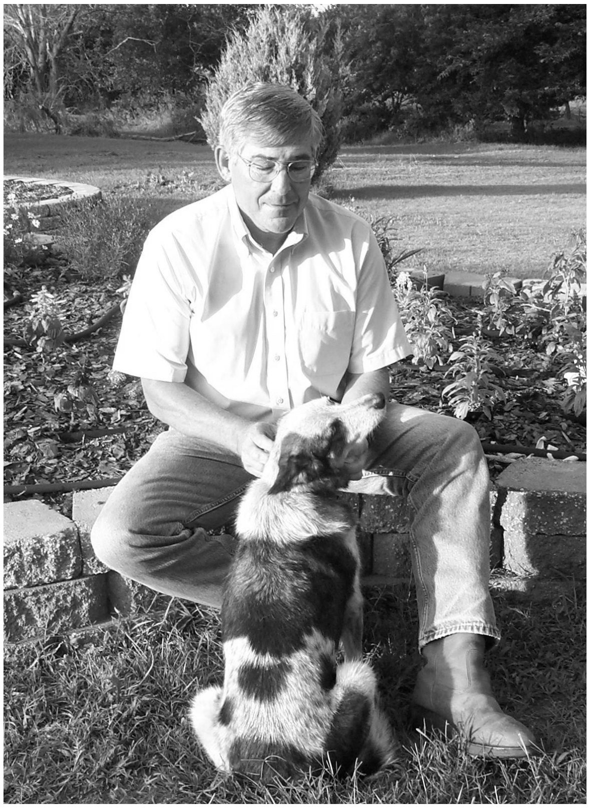

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