

Clark University

Clark Digital Commons

Faculty Works

Scholarly Collections & Academic Work

1986

Ethology and the Birth of Comparative Teleonomy

Nicholas S. Thompson

Follow this and additional works at: <https://commons.clarku.edu/facultyworks>

Ethology and the birth of comparative teleonomy

Nicholas S. Thompson

1 INTRODUCTION

At a recent conference, some of my colleagues attempted to trace contemporary ethology to themes in its past and thereby to project its future. This enterprise was based on the assumption that the development of animal behavior science has been and will be incremental and that change must be of the continuous, rather than of the discontinuous variety.

The assumption seems gratuitous. In the first place, the most widely regarded philosophy of science of the day holds that important change in sciences is discontinuous. Thomas Kuhn in his ubiquitous Structure of Scientific Revolutions (1970) argues that sciences consist of paradigms, i.e., systems of dogma, methods, and people. Significant change occurs when one paradigm is overturned and a new paradigm replaces it bringing its own dogma, its own methods, and its own patterns of association among its practitioners. The change from old to new is not evolutionary, but revolutionary. The new paradigm is not just novel. It is totally out of keeping with the old. Consequently, if we believe that the study of animal behavior is in a period of important change and if we believe Kuhn's account of important change, then we would not expect change to be continuous, nor should we expect to be able to project the future of animal behavior study from its past.

And indeed, much about the conference suggested that a period of disorderly change was in progress. Implicitly, the future of the discipline as such seemed in question. The papers at the conference were remarkably heterogeneous, showing very little in the way of common themes or concerns. Few of the people at the conference thought of themselves unambiguously as ethologists, but rather identified themselves as behavioral ecologists or sociobiologists or developmental psychologists or any of several other related specialties. While one speaker (Hinde 1985) was able to project the influence of ethology upon other disciplines, and another (Fentress 1985) was able to project the effects of other disciplines upon the future of ethology, few were able to say much about the effects of the past of ethology upon its own future.

This experience convinced me that the field of animal behavior is in the midst of a paradigm shift and ethology is near the end of its life. Thus, ethology might be regarded not as a continuing entity, but as a discipline which arose at a particular time, strove to achieve certain conceptual ends,

*Relevance of models and theories in ethology, Ed by Raymond Campan & René Zayan
Privat, I.E.C., Toulouse, 1986, pp. 13-23.*

used characteristic methods to achieve those ends, and, having achieved them, quietly passed away.

I have argued elsewhere (Thompson 1976) that such patterns of birth, maturation and decline in disciplines are based on the discovery and resolution of contradictions between conceptual categories. Human beings need to sort things into categories; and when that sorting process is frustrated for some reason, intellectual activity is generated. From this activity springs up new research activities, disciplines, departments, agencies, societies, and conferences. This analysis suggests that I should find at the core of ethology a contradiction which became evident about the time that ethology emerged and which was resolved about the time that ethology came to an end.

What follows is an attempt to look at ethology as if it were a completed endeavor and to celebrate its achievements. In this attempt, I have emphasized some aspects and de-emphasized others. Some readers may object to this reconstruction. For instance, some may disagree that ethology was "teleonomic", citing as evidence the frequent references in the literature to such constructs as endogenous energy flows. These constructs did run counter to the teleonomic mainstream of ethology. But they do not change the essential fact that ethology committed itself to the use of concepts derived from the description of behavior in its natural context. Thus, while ethologists often mistook their own descriptive concepts for explanatory ones, we in retrospect need not do so. We can see that the primary force of these concepts, no matter how internally or mechanically they may have been expressed, was to characterize and represent higher-order patterns in behavior in relation to its circumstances.

What emerges from this reconstruction is a picture of ethology which makes clear why it emerged when it did, what it accomplished, why it died when it did, and where we former ethologists should now turn in our search for fruitful contradictions.

2 THE NATURE OF ETHOLOGY

Ethology sought to discover the origins of design in behavior. It arose in the early part of the twentieth century in response to Darwinism. Darwinism, by eliminating supernatural origins as a cause of natural design posed the problem of reconciling design in nature with the material principles of natural selection and physiological activity. Two extreme responses to the Darwinian challenge were current in the literature at the time ethology arose (Lorenz 1950). A vitalistic tradition, most clearly displayed in the work of McDougall, traced design in animal behavior to the mind of the animal itself. The animal was thought to behave in a designed manner because instincts directed it toward broad functions as goals. A mechanistic tradition, identified with the writings of Watson and other American behaviorists, effectively denied the existence of design in the animal behavior by attributing it to contingencies in the environment. Environmental contingencies impressed themselves upon the nervous system of the

animal as molecular elements of habit which made behavior consistent with those contingencies. Ethology struck a balance between these two extremes. It sided with the mechanistic tradition in asserting that behavior should be analysed into units more molecular than broad functions. It sided with vitalism in granting to behavior qualities of directedness of its own. Thus it strove to analyze behavior into molecular patterns of directedness.

Ethology was a teleonomic science (Thompson 1986). Teleonomy is an "objectively teleological," realist, and holistic approach to the study of biological phenomena. "Objective teleology" is a stance offered by the philosopher Albert Hofstadter (1941) which treats teleology not as an explainer of behavior but as a describer. Something about goal-directed behavior inspires us to see its ends as controlling its means. Whether or not in fact those ends are controlling those means, the behavior looks as if they are and it is to this appearance that the term "teleology" is to be applied. The objectively teleological approach to design suggests that whatever or whoever the designer is, he, she, or it leaves his, her, or its imprint upon the world. It is to this imprint, that the objective teleologist assigns the word "design." For our present purposes, "design" refers to whatever it is about a designed object that makes it seem so. No other interpretation of the word will permit a coherent reading of what follows.

A teleonomic approach is a "realist" approach. Design is not only in the eye of the beholder. Design is a property of the world. It is out there. Not all parts of all organisms may possess it, not all methods may reveal it, not all observers may believe in it, but still it is there: a characteristic of natural things that remains ready to be revealed.

Finally, a teleonomic approach is "holistic". Design is a higher-order property of things. A single object can be consistent or inconsistent with a design, but it cannot define a design. We should look for design in consistent patterns of relationship among things, not in the things themselves.

3 THE CONCEPT OF NATURAL DESIGN

The key teleonomic concept relevant to the history of ethology is the property of behavior called "natural design" (Thompson 1986). Defined teleonomically, design is an association between two arrays, an array of structures and an array of uses. A mechanic's tool box contains specialized instruments for each of the operations the mechanic must perform, each tool fitted to the form of a particular type of bolt, screw, socket or fitting. Looking at the toolbox, one might say that a particular wrench is well designed for turning a particular bolt. As design is here understood, this statement means more than saying that the wrench turns the bolt. Several tools in the box may be effective in that respect. It means that there is in general a relationship between the form of the tools in the box and the tasks they are used for and that the wrench is exemplary of that relationship.

Natural design is an association between an array of forms of organisms and the array of their circumstances. For in-

stance, mammals are usually colored to match the background against which they live. A snowshoe hare is well concealed against a snowbank. But we would be wrong in saying that the snowshoe hare is designed to be concealed against a white background if [1] all backgrounds were white and mammals differed in color or if [2] all mammals were white and backgrounds differed in color or if, [3] in general, there were no relationship between background and color. What makes the snowshoe hare naturally designed is that there is, in general, an association between background and pelage color and the hare exemplifies that association.

Natural design in behavior is an association between an array of activities and an array of circumstances in which these activities are deployed. Behavioral design takes three forms, each defined by a different set of arrays. When one considers the array of environments in which different animals live, the array of different behaviors deployed by animals in those environment, and observes an association between the environments and the behaviors deployed, then one speaks of behavioral adaptation. The state of affairs to which a particular behavior is matched is said to be its function. For instance, the prey-catching techniques of different species of predator are systematically related to the type of prey they hunt. When we say that the cheetah is adapted for hunting fleet-footed ungulates, we mean not only that cheetahs catch these ungulates by running them down, but that their hunting technique is exemplary of the general relationship between the technique of the hunter and the behavior of the hunted. The hunter's behavior is adapted to the behavior of the hunted and catching prey of that type is its function.

The second form of behavioral design manifests itself when one examines the array of circumstances encountered by a maturing organism as it ages and an array of behaviors that it typically deploys in these circumstances. In this case, one speaks of behavioral development. For instance, at every stage of its maturation, the young mammal and its conspecifics display toward one another behaviors which are characteristic of its age and appropriate to its situation. When we say that a young organism is developing, we mean that it is moving through such a sequence of age-specific behaviors.

Another form of behavioral design is revealed when one examines the array of behaviors deployed by an individual animal during its daily round in association with the array of circumstances in which those behaviors are deployed. Here, one speaks of purpose. Purpose implies two nested levels of design. At the more inclusive level, behaviors are grouped by their association with particular circumstances into modalities called "purposes." Modalities are defined by situations that terminate them called goals. When the goal situation occurs, the organism shifts to another modality. Within each modality, behaviors are associated with different degrees of approximation to the goal-situation. We can recognize classes of behavior which are typically deployed in the absence of food, in the presence of sexually stimulating odors, and in the presence of dangerous opponents. Within each of these classes, we can recognize patterns of association between the proximity of the appropriate goal-situation and the behavior that is deployed.

4 ETHOLOGY AND NATURAL DESIGN

Ethology focused on the origins of behavioral adaptations. For a behavioral adaptation to exist, it has to arise in at least three senses: it has to arise in the evolutionary history of the species, it has to arise in the developmental history of the individual organism, and it has to arise in the immediate circumstances in which it is deployed. Three sorts of questions encompass motivated ethological investigations, each of which understands origins in a different time frame.

How do adaptations arise in phylogeny?

How do adaptations arise in ontogeny?

How do adaptations arise in day-to-day behavior?

During its career, ethology employed characteristic methods to discover definitive answers to each of these questions.

4.1 Phylogenetic Origins of Adaptations

Darwin's theory of natural selection tells us that adaptation arises because of the differential reproduction of alternative types of organisms. From a teleonomic perspective, this amounts to the assertion that the agent of natural selection (i.e., the factor which presides over differential reproduction) is identical to the behavior's function (i.e., the factor to which the behavior is adapted). Although the assertion is clear enough, enormous practical obstacles stand in the way of testing it. The course of evolution of a behavior is a unique historical event, and no experiment in the present can recreate precisely the circumstances of the past. To test the theory, therefore, we have to assume that the agents which are currently selecting an adaptation are the same agents that selected it in the past. Granting this assumption, this assertion can be given empirical reference and tested.

Here are two classical examples:

Gulls which nest on flat surfaces characteristically concern themselves with nest cleanliness more than gulls which nest on cliffs. In particular, the habit of removing eggshells from the nest soon after hatching seems to be an adaptation to nesting on the level where visually searching predators are a constant hazard. The observer adds open eggshells to natural nests, attempting to duplicate the situation that would occur if the gull were prevented from removing eggshells. Predation occurs more in those nests to which the shells have been added (Tinbergen et al. 1963).

Many small fish have large potential predators that eat by gulping. Some such fish have sharp dorsal spines which appear to be a defensive adaptation against their predator's feeding technique. The investigators tested the proposition that the predators were the agent of selection of the spines by cutting the spines off some of the small fish. Despined fish were taken more frequently by predators than spined fish (Hoogland et al. 1957).

In each case, the investigation strengthens the conclusion that the agent of natural selection is the function of the behavior or structure. Eggshell-removal looks like an adaptation to visual predation, and the experiment indeed suggests that eggshell-removal diminishes such predation. Having sharp spines looks like an adaptation to avoiding predation by large predators, and indeed the experiment suggests that having such spines decreases such predation.

4.2 Ontogenetic Origins of Adaptations

Some of the most persuasive examples of behavioral design are the coordinations that exist between parents and offspring during the course of the latter's maturation. The vitalistic interpretation of these coordinations is that the parent and offspring innately know when to perform the behaviors necessary for the maturation of the young. The mechanistic interpretation is that contingencies in the environment determine the timing. These different sorts of interpretations have led to a sterile nature/nuture conflict, one school finding the origins of adaptation in the genes, the other in experience.

The classical ethological study reveals an intermediate chain of events. The parent or the offspring know something but it is not how or when to perform the functionally appropriate response. The animal strives to perform the response to a class of conspecifics defined by particular experiences. Two more classics:

When her lamb is born, the ewe licks it thoroughly and thereafter permits it, and only it, to approach her for nursing. The investigator interferes by removing the lamb just after birth and returning it to the mother a few hours later. The mother rejects it and will not permit it to nurse (Hersher, Richmond and Moore 1963).

Within a day of hatching, a young gosling faithfully follows its mother across the barnyard and will not follow other species or even other geese of the same species. The investigator interferes by removing goslings from the mother immediately after hatching. In the absence of the mother, the goslings follow the investigator around the barnyard. After a few hours, the goslings are returned to the mother, but they will not follow her and will follow only the investigator thereafter (Lorenz 1957).

Among flock-living creatures such as geese and sheep, the close association of parent and offspring is a characteristic adaptation. One might suppose that parents and offspring recognise each other as individuals. The first experiment demonstrates, however, that the ewe seeks to care for lambs that share the odor of the lamb whom she licks after giving birth. The second experiment demonstrates that the gosling seeks to follow that large moving object that it saw in the first few hours after hatching. Thus, the functional appropriacy of the present responses arises out of the interaction between prior behavioral propensities and information which these propensities made available.

4.3 Day-to-Day Origins of Adaptations

A characteristic ethological experiment is one in which an example of adaptation in the behavior is examined to reveal what the organism is actually trying to do. The procedure involves making a substitution of some sort in the environment of the organism so that the organism achieves its goals but does not achieve the functional state of the behavior. The archetype of this sort of investigation is Lorenz and Tinbergen's study of the eggrolling of the grey-lag goose.

A goose is observed to roll an egg into its nest. Upon completing the rolling procedure the goose typically settles itself into its nest and behaves as if it is "satisfied" that it has returned the egg to the nest. The observer notes that if the egg escapes from the bill during the rolling procedure, the goose still completes the eggrolling motions and still behaves as if the egg has been returned to the nest (Lorenz and Tinbergen 1957).

Many geese are ground-nesting birds. Among such birds, a response to eggs outside the nest is characteristic, whereas among tree- or cliff-nesting birds, eggs outside the nest may be ignored or even destroyed. The egg rolling behavior is an adaptation in the sense that it is well matched to its circumstances. Given that it is an adaptation, one might suppose that the goal of the goose is to get the egg back in the nest. But the experiment reveals that this is not the case. It shows that the goal of the goose is to get its beak in a particular relationship to white round objects outside the nest. Once that relationship is achieved, the eggrolling reflex occurs and the goose is satisfied, no matter what happens to the egg. Fortunately for [but unforeseen by] the goose, the only largish white object which regularly occurs outside its nest in its natural habitat is a egg from its own nest.

Another familiar example:

A robin attacks a fellow robin which has a red breast at the boundary of their territories. The investigator traps one of the combatants and substitutes a bit of red fluff on a bit of wire attached to a twig. The remaining robin attacks this artifact with the same vigor with which it attacked its neighbor only a few moments before (Lack 1965).

An English robin is a territorial bird. Under its ecological circumstances, exclusion by males of other males of the species is a characteristic adaptation. One might suppose that individual males might try to achieve this adaptation as a goal, but the experiment demonstrates that the robin's goal is only to eliminate the stimulus "red tuft on stick." Fortunately for the robin, the only stimulus in its natural environment which is consistent with the configuration "red tuft on stick" is another male robin.

4.4 The Accomplishments of Ethology

Taken together, such investigations reveal general teleonomic laws concerning the origins of natural design in behavior. The first of these laws relates natural selection to behavioral adaptation. It asserts that whatever the organism is adapted to will be found to be the thing that is selecting it. The law is difficult to summarize in a single phrase and might, therefore, be known simply as Tinbergen's Law.

A second law concerns the origins of design in ontogeny. It claims that whenever behavior is found to be well-designed for a particular stage of ontogenesis, its design will be found to have arisen dialectically from the interaction of the organism in the previous stage of ontogenesis with the environment at that stage. This law might appropriately be known to future animal behaviorists as the Law of Dialectical Ontogenesis, or as Schneirla's Law.

The third law might appropriately be known as The Law of Short Sighted Striving, or Lorenz's Law. The Law has three parts. The first is that goals of an animal's behavior may not be identical to its functions. That is, whatever an animal seeks to achieve by its behavior may not be the situation to which the behavior is adapted. The second part is that the achievement of goals results in the achievement of functions. In other words, even though the organism does not anticipate in any sense, the achievement of the functional situation, nonetheless its striving does reliably produce that situation. The third part is that the connection between the goal-situation and the function-situation is due to a fact of nature. In other words, some circumstance in the typical environment of the species assures that achievement of the goal of a purpose results in the achievement of the functional situation.

These generalities are so banal to the field of ethology that readers may be reluctant to dignify them with the status of laws. But of course, banalities are the substance of laws. And these laws are banalities only because ethologists have worked for sixty years or more to make them so. The discovery and documentation of these laws constitute the great achievements of the field of ethology. By granting them the status of laws, we not only honor them, we also consolidate them in our own minds and in the minds of future students of animal behavior.

WHERE DO WE GO FROM HERE?

What I have argued so far is that ethology as a science had a discrete lifetime. It arose from contradictions between the evidence of design in animal behavior and the material principle of natural selection offered by Darwinism to explain it. It ended as a discipline because it resolved the contradiction by saying that design in behavior arose from three sources: from natural selection, from the ontogenetic dialectic, and from the short-sighted striving of the organism.

If the view of science that I propose is correct, then we should look for the future of animal behavior in its present contradictions. One such contradiction is clearly in view and has clearly formed the basis for the field of Sociobiology. Natural selection is a competitive principle yet animal social behavior is very often cooperative. Sociobiology is the field which attempts to reconcile the complex cooperation evident in social organizations with the simple competitive principle of natural selection. Sociobiologists view genes as elementary units of self interest and they attempt to explain the many and varied forms of cooperation in terms of these elementary units.

Another equally interesting contradiction has not been so thoroughly explored. The fact is that much of animal behavior does not seem to be well-designed. The discovery of the Law of Short Sighted Striving in animals led immediately to a concern with five naturally occurring anomalies in the design of behavior. To see why this concern developed we need to examine in greater detail the structure of social purposes. We have observed that a purposive organism's behavior is organized into several modalities, each terminated by a goal situation. These modalities correspond to what a non-teleonomist would call a motive, but modalities, unlike motives, carry with them no trace of explanatory intent. Within the modalities, circumstances and behaviors are arrayed in terms of their proximity to the goal situation. An organism characteristically perseveres within a modality until the goal situation is achieved and/or the circumstances are changed.

When purposes are asocial, then the circumstances relevant to a particular modality are states of affairs in the environment. But when purposes are social, then the circumstances are generally the behaviors of other animals. Since most animal behavior is purposive, then most social interactions consist in a meshing between the purposive arrays of two animals, such that the circumstances for one organism are the behaviors of the other, and vice versa. These linkings of arrays can be symmetrical or complementary. An example of a symmetrical meshing or arrays would be two animals engaged in aggression. An example of a complementary meshing of arrays, would be one animal attacking another which is appeasing or fleeing.

As with asocial behavior, in social behavior the two organisms tend to remain in a particular modality until one or both of them achieves the goal state. In fact, this is characteristically true with social purposes because the perseverance of each party within its modality, confirms the other in its modality. That the meshing of the behavior of two animals is characteristic of normal design, suggests that exceptions to this meshing would be anomalous. If for instance, an animal were to direct its behavior to another animal with which it is not meshed, or to direct a behavior out of its present modality to the animal with which it is meshed, such conduct would seem anomalous.

Five such anomalies have been considered. These are intention, displacement, redirection, and vacuum activities and play. Each of these phenomena is defined by a different anomalous relationship between the form of the behavior and the modality in which the organism is operating when the behavior occurs.

Intention movements are incomplete fragments of behavior appropriate to the modality in which the animal is operating at the moment. They are anomalous in that they do not appear to advance the organism toward the goal-situation. Displacement activities are behaviors from one modality which occur when an animal is operating in another modality. Redirection activities and vacuum activities are behaviors from the appropriate modality which are directed toward an inappropriate object, an object with which the behavior is not enmeshed at the moment.

The most familiar and widely studied of design anomalies in behavior is play. Play bears some resemblance to intention movements and to vacuum and redirection activities. In play the modality structure of behavior breaks down (Bekoff 1976). The animal may switch rapidly from modality to modality, say from aggression to flight. Or behavior may persist in a single modality for several seconds, only to change to another without achieving the goal object. Or it may persist within a modality for an indefinite period of time but not progress toward the goal situation in the normal way (Mitchell and Thompson 1986).

These anomalies suggest that a contradiction may exist between behavior as we find it and the concept of natural design. Ethologists may have failed to resolve this contradiction because they wrongly saw it as a problem of explanation, rather than a problem in description. Thus, a fruitful direction for the future of animal behavior might be in the detailed analysis of the design of behavior. Such a program of study would raise such questions as, in what way and under what circumstances is behavior well-designed? When is it ill-designed? The explicit study of design would lead animal behaviorists to consider the structure of the relationship between behavior and its circumstances. It would be a teleonomic program in two ways. First, it would seek to reveal the structure of behavior, not simply to describe its fragments. Second, it would engage in explicit description, rather than pseudo-explanation.

What name shall we give the new field? Why not call it "comparative teleonomy" and define it as the study of the design properties of human and animal behavior?

Acknowledgments. Pat Bateson, Emil Menzel, Peter Klopfer, Bob Mitchell, James Laird, John Fentress, Peter Lipton and Dan Shartin all provided much needed editorial advice on very short notice. Any who saw earlier versions of this essay will know the degree to which I am in their debt.

REFERENCES

- BEKOFF, M., 1976. Animal play: problems and perspectives. In: P.P.G. BATESON and P.H. KLOPFER (Editors), *Perspectives in Ethology*. pp. 165-183.
- FENTRESS, J.H., 1985. *Ethology and the neural sciences*. Paper given to the 19th Ethological Congress, Toulouse, France.

- HERSHER, L., RICHMOND J.B. and MOORE, A.U., 1963. Maternal behavior in sheep and goats. In: H.L. RHEINGOLD (Editor), *Maternal Behavior in Mammals*. Wiley, London, England, pp. 203-232.
- HINDE, R.A., 1985. Ethology and the social sciences. Paper given at the 19th Ethological Congress, Toulouse, France.
- HOFSTÄDTER, A., 1941: Objective teleology. *The Journal of Philosophy* 38: 29-39.
- HOOGLAND, R., MORRIS D. and TINBERGEN, N., 1972. The spines of sticklebacks as means of defence against predators. In: P.H. KLOPFER and J.P. HAILMAN (Editors), *Function and Evolution of Behavior*. Addison-Wesley, Reading, Massachusetts, pp 104-118.
- KUHN, T.S., 1970. *The Structure of Scientific Revolutions*. University of Chicago Press, Chicago, Illinois, 210 pp.
- LACK, D., 1965. *The Life of the Robin*. Witherby, London, 234pp.
- LORENZ, K.Z., 1950. The comparative method in studying innate behaviour patterns. In: P.H. KLOPFER and J.P. HAILMAN (Editors), *Function and Evolution of Behavior*. Addison-Wesley, Reading, Massachusetts, pp 3-36.
- LORENZ, K., 1957. Companionship in bird life. In: C. SCHILLER (Editor), *Instinctive Behavior*. International Universities Press, New York, New York, pp 83-128.
- LORENZ, K. and TINBERGEN, N., 1957. In: C. SCHILLER (Editor), *Taxis and instinctive action in the egg-retrieving behavior of the greylag goose*. *Instinctive Behaviour*. International Universities Press, New York, New York.
- MITCHELL, R.W. and THOMPSON, N.S., 1986. Deception in play between dogs and people. In: R.W. MITCHELL and N.S. THOMPSON, (Editors), *Deception*. SUNY Press, Albany, New York, pp. 183-192.
- THOMPSON, N.S., 1986. Deception and the concept of natural design. In: R.W. MITCHELL and N.S. THOMPSON (Editor), *Deception*. SUNY Press, Albany, New York, pp 53-66.
- THOMPSON, N.S., 1976. My descent from the monkey. In: P.P.G. BATESON and P.H. KLOPFER, (Editors), *Perspectives in Ethology*. Plenum, New York, New York, pp. 221-230.
- THOMPSON, N.S., 1986. The Missappropriation of Teleonomy. In: P.P.G. BATESON and P.H. KLOPFER, (Editors), *Perspectives in Ethology*. In press.
- TINBERGEN, N., BROEKHUYSEN, G.J., FEEKES, F., HOUGHTON, J.C.W., KRUK, H. and SZULC, E., 1963. Eggshell removal by the Black-headed Gull, *Larus ridigundus* L.; a behaviour component of camouflage. *Behaviour*, 19, pp 74-117.

Address: Departments of Psychology and Biology, Clark University, 950 Main Street, Worcester, MA 01610, U.S.A.