

The Levels of Analysis

Much confusion still exists among biologists about how to answer questions of the general form 'Why does animal A exhibit trait X?' A recent, conspicuous example of this confusion is the debate about why human females have clitorises. Gould (1987a) argued that clitorises are a developmental side-effect of selection on males for penises and, following Symons (1979), that clitoral orgasms are not adaptations. Alcock (1987) responded that since clitorises are neither inert nor imperfectly formed, as he expected under Gould's hypothesis, functional explanations should be sought. Alcock (1987, page 4) cited several possibilities (see Smith 1984), and championed the idea that clitorises facilitate orgasm which, in turn, 'acts as a mechanism of discriminating mate choice and paternity control by females'. In his rebuttal, Gould (1987b, page 4) claimed Alcock 'misunderstood my major point', that it is 'logically incorrect (to) equate current utility with reasons for historical origin'.

There are two reasons why Gould and Alcock disagree, yet seem to talk past each other. The first is semantic. For Gould (1987a, b), clitorises must be 'non-adaptive' structures if they originated evolutionarily as a developmental by-product of selection in another context; for Alcock (1987), in contrast, clitorises and orgasms are 'adaptations' if they seem designed to enhance reproductive success. Although Gould's hypothesis is silent about the relationship of the clitoris to female fitness, he (1987a, page 18) pitted his hypothesis directly against explanations based on differential reproduction (e.g. Hrdy 1981), and dismissed the latter. This points up the second and more basic reason for the disagreement, namely that clitorises, like other aspects of the phenotype, can be explained from several different, but not mutually exclusive, perspectives. Failure to separate clearly these 'levels of analysis' has led both to this terminological misunderstanding and to unwarranted polemics.

Confusion over explanatory levels and ensuing inconclusive arguments nag all branches of biology, and the literature is full of examples. A classic is the so-called 'nature-nurture' controversy (e.g. Lorenz 1950 versus Lehrman 1953), which arose over whether certain behaviours of chicks are innate 'or' acquired through experience. After two decades of unenlightening debate, it became apparent to Mayr (1961), Tinbergen (1963) and Lehrman (1970) that the lack of consensus was mainly due to semantic and conceptual issues, rather than to discrepancies of fact. In his 1961 paper, Mayr observed that life scientists conceptualize research questions in two ways: functional biologists study

'proximate' causality, and evolutionary biologists concentrate on 'ultimate' causes. Proximate factors operate in the day-to-day lives of individuals, and ultimate causes derive from evolutionary history. Tinbergen (1963) suggested that each of these categories should be subdivided. Thus, proximate or 'how?' questions require investigations of both individual ontogeny (e.g. effects of age and experience) and physiological substrates, including neuronal, hormonal and biochemical mechanisms. Ultimate or 'why?' questions require understanding both evolutionary origins and current adaptive value. Answering the former entails unravelling the history of phenomena in geological time, while the latter involves comparing the fitness consequences of naturally occurring variants in ecological time.

It has recently become apparent that, in behaviour at least, there is a fifth research approach which was not specifically considered by Mayr (1961) and Tinbergen (1963). It deals with presumed mental processes, both cognitive and emotional. These were discussed in terms of 'consciousness' by Romanes (1883), 'hypothetical constructs' by MacCorquodale & Meehl (1948), 'drives' by Lorenz (1950) and 'awareness', 'thinking', and 'motivation' by several recent authors (e.g. Griffin 1984; Colgan 1986). Although animals' mental capabilities are, ultimately, based on physiological processes, considerations of mental performance often yield hypotheses that, given our current state of knowledge, do not fit comfortably into purely mechanistic interpretations. For example, studies of whether or not honey bees, *Apis mellifera*, possess cognitive maps and employ landmarks in returning home from unfamiliar locations (Gould 1986), whether or not parrots (Pepperberg 1987) or apes (Savage-Rumbaugh 1984) can use human symbols to characterize novel objects, and how animals make mate choice or optimal foraging decisions (Shettleworth 1984) yield insights into mental function that are not immediately reducible to physiological processes. To specify hypotheses in this unique type of inquiry, I use the generic term 'cognitive processes'.

In summary, there are four different levels of analysis: evolutionary origins, functional consequences, ontogenetic processes and mechanisms; the latter includes both cognitive processes and physiological processes. Every hypothesis in biology is subsumed within this framework; competition between alternatives appropriately occurs only within and not among levels (Mayr 1982, pp. 59-77). This means that there are multiple types of 'correct' answers to any question about causality. Which category of answer is most satisfactory or interesting is a matter of training and taste; debating the issue is usually fruitless.

Consider, for example, the question: 'Why do male canaries sing their particular songs?' In terms of physiological processes, alternative hypotheses might implicate activational versus organizational hormone mechanisms, or fixed versus variable neuroanatomical structures (see Konishi 1985). Regarding cognitive processes, perhaps singing males are 'angry' about territorial intrusions, or 'amorous' toward potential mates (Mulligan & Olsen 1969). Alternative ontogenetic processes could be learning by chicks of paternal songs versus vocal reproduction of an unlearned template (reviewed in Kroodsma & Miller 1982). The functional consequences of song might be either attracting a mate or repelling rivals (Catchpole 1982). Finally, in terms of evolutionary origins, maybe simple, repetitive songs characterize all cardueline finches, or else canaries' songs are unique and

highly derived, relating to recent speciation in the genus *Serinus* (see Payne 1986). All these hypotheses are testable and five of them might be right simultaneously; conversely, all or any of them may be wrong.

Although most of the conceptual advances regarding levels of analysis occurred 25 years ago, even today only a minority of biologists explicitly categorize their hypotheses this way. Partly as a result, few structures or behaviours are understood from all the possible perspectives. Further, many acrimonious debates in evolutionary biology apparently originated as supposedly alternative hypotheses which were, in reality, on different analytical levels (Table I). One reason the protagonists in such debates can act so self-righteously is that each may, in fact, be correct; yet this does not necessarily jeopardize any hypotheses at other

Table I. Some recent controversies generated primarily because the author of hypothesis A, an explanation of evolutionary origin, mechanism, or ontogeny, mistakenly pitted it against hypothesis B, an explanation of functional consequences (i.e. effects on fitness)

Structure or behaviour	Non-alternative explanatory hypotheses*	
	A	B
Sexual monomorphism in hyenas (<i>Crocuta</i> spp.)	Male-like genitalia arose as a non-adaptive by-product of high testosterone levels associated with female dominance (Gould 1981) (evolutionary origin)	Male-like genitalia are used in signalling and help females compete effectively with males at carcasses (Hamilton et al. 1986) (functional consequences)
Alarm calls in ground squirrels (<i>Spermophilus</i> spp.)	Adult females call because of hormonal correlates of lactation (Shields 1980) (mechanism: physiological processes)	Adult females call to warn close relatives of danger (Sherman 1980) (functional consequences)
Senescence	The result of an accumulation of defects in macromolecules (Kirkwood & Holliday 1979) (mechanism: physiological processes)	The result of extrinsic mortality factors and rapid reproduction early in life (Williams 1957) (functional consequences)
Infanticide in langurs (<i>Presbytis entellus</i>)	Males who take over troops are 'agitated' over possible attacks by rivals, and they 'redirect' their aggression at infants (Mohnot 1971) (mechanism: cognitive processes)	Males who take over troops eliminate the progeny of their predecessor and then mate with the dead infants' mothers (Hrdy 1974) (functional consequences)
Incest avoidance in humans	Parents teach offspring to avoid sex with siblings (Kitcher 1985) (ontogenetic processes)	Individuals gain by avoiding the deleterious genetic results of close inbreeding (Alexander 1974; Wilson 1978) (functional consequences)

* Because hypotheses A and B are on different levels of analysis, they do not legitimately compete as alternatives; both A and B, either one, or neither may be correct.

analytical levels. This is what Lehrman meant when he wrote (1970, page 28) 'the clearest possible genetic evidence that a characteristic of an animal is genetically determined in the sense that it has been arrived at through the operation of natural selection does not settle any questions at all about the developmental processes by which the phenotypic characteristic is achieved during ontogeny'. The point is that the controversy over the clitoris and the others listed in Table I did not need to happen. Such debates can only be sustained as real disagreements by ignoring the levels-of-analysis issue.

Gould (1987b, page 6) ended his rebuttal with the statements that 'good science needs, above all, testable hypotheses of all feasible types — including developmental and adaptationist' but 'if anything... developmental explanations are more expansive and operational than the necessarily fruitless and untestable adaptationist speculations that continue to permeate our literature'. Why Gould believes that developmental hypotheses about evolutionary origins are generally more powerful, parsimonious and testable than 'adaptive' explanations (based on differential reproduction) is unknown. Also unclear is why Gould refuses to acknowledge that his hypothesis, if it were extrapolated to the level of functional consequences, predicts that the clitoris is essentially neutral for female reproduction: a testable and falsifiable proposition (Alcock 1987). Gould's first statement is easy to agree with, so long as the hypotheses that are tested as alternatives are on the same level of analysis, and explanations at one level are viewed as complementing, not superseding, those at another.

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Intergenerational Conflict in Gulls

There is increasing evidence of a surprisingly high incidence of adoption of foreign chicks in some of the larger *Larus* gulls (Graves & Whiten 1980; Holley 1981, 1984; Pierotti & Murphy 1987). In relation to the herring gull, *Larus argentatus*, I suggested that adoptions arose because parents were unable to recognize their own young, a factor that may not have been important in the original environments in which the species evolved but that is maladaptive in current densely populated flat ground colonies (Holley 1984). Pierotti & Murphy proposed an alternative hypothesis, intergenerational conflict, which in parts is similar to the 'vagrant chick hypothesis' of Mock (1984). They said that in such a conflict there would be selective pressure on adults to recognize offspring, but if there is a real advantage to a chick that succeeds in getting adopted a countering selection force could favour those chicks that can foil the adults' ability to recognize their own offspring. On the basis of the hypothesis they made a number of predictions of which the third and fourth are relevant here. In

their third prediction they stated that 'chicks seeking adoption should attempt to establish themselves in nests where they are the largest chick because their chances of dominating resident chicks will increase', and in their fourth prediction they stated that 'adult gulls should be more willing to adopt when the cost of adoption (in time and energy) is low, i.e. during good as opposed to poor years for food'.

When discussing their results Pierotti & Murphy said that all their predictions concerning the interaction between adults and offspring seeking care had been confirmed by their data. That is not correct. As to predictions (3) and (4) their results were equivocal. They did not show that chicks seeking adoption attempted to establish themselves in nests where they were the largest chick, but that it was in such nests that adopted chicks were found. Similarly, they did not show that adult gulls were more willing to adopt in good food years, but that there were more adoptions in such years. In each case the mediating factor could have been something altogether different from that predicted. That factor might well be the behaviour of the natal broods on the territories of adopters.

Whilst there is reason to doubt the ability of herring gull parents to recognize their chicks, there is no doubt of the ability of chicks to recognize their parents and their siblings (Noseworthy & Lien 1976; Knudsen & Evans 1986). Chicks do vigorously attack other chicks and even adults trespassing onto their territory (personal observation). We do not know, because Pierotti & Murphy did not address the question, whether runners choose territories on which they will be the largest chick, or whether they visit territories more or less at random and stay on those where the adults do not reject them and the natal brood are not large enough to evict them. Likewise, we do not know whether in years of poor food availability adults are less inclined to adopt, or whether their own offspring resist even more strongly than usual the intrusion of strangers into their ranks. The authors, having pronounced their hypothesis and the predictions which it would suggest, have fallen into the trap of failing to design unequivocal tests, thereby leaving a vulnerable hypothesis.

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