Instituto Juan March
de Estudios e Investigaciones

6

CENTRO DE REUNIONES
INTERNACIONALES SOBRE BIOLOGÍA

Workshop on

Behavioural Mechanisms in Evolutionary Perspective

Organized by

P. Bateson and M. Gomendio

J. R. Alberts
G. W. Barlow
P. Bateson
T. R. Birkhead
J. Carranza
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F. Colmenares
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J. Maynard Smith
A. P. Møller
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SUMMING UP

INTRODUCTION

P. Bateson

Introduction

Patrick Bateson

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In their time, the founding fathers of ethology were particularly successful, partly because they brought to behavioural biology a coherent theory of how behaviour is organised and partly because they were interested in what behaviour was for. Their functional approach marked them out as being quite different from the comparative psychologists who had been emphatically upstaged. Niko Tinbergen was as clear as anybody about the distinctions that should be drawn between "how" and "why" questions, but he saw the value of keeping the two approaches in play at the same time (see Dawkins 1989).

By the early 1970s, ethology itself was ripe for take-over. Its Grand Theory was in ruins and the much hoped for understanding of the links between behaviour and underlying mechanisms was still fragmentary. Meanwhile, field studies relating behaviour patterns to the social and ecological conditions in which they normally occur led to the enormous popularity and success of behavioural ecology in which an understanding of mechanisms played very little part.

Sociobiology moved into the available space, bringing to the study of behaviour important concepts and methods from population biology, together with some grandiose claims of its own. Imaginations were captured by the way the ideas from evolutionary biology were used and the majority of aspiring graduate students wanted to work on a problem in this new area. The appeal of evolutionary theory, in which sociobiology was embedded, was that it seemed to make a complicated subject manageable (see Barlow 1989). The drawback to the subject as a whole was that large chunks of behavioural biology, which had been central concerns of ethology, were deemed to be irrelevant or uninteresting. Few students interested in whole animals wanted to work on how behaviour develops or on how it is controlled. For many years, therefore, issues to do with mechanism were largely ignored. Recently, however, a start has been made on rebuilding the atrophied links between the "why" and the "how" questions.

Asking *what* something is for is never going to reveal directly the *way* in which that thing works. But the functional approach does help to distinguish between independent mechanisms controlling behaviour and can lead fruitfully to the important controlling variables of each system. This is important in the design of experiments in which, inevitably, only a small number of independent variables are manipulated while the others are held constant or randomised. The experiment is a waste of time if important conditions that are going to be held constant are badly arranged. A functional approach can provide the knowledge that prevents expensive and time-consuming mistakes.

Those who worked on optimal foraging have appreciated that their work raised important issues about how behaviour is controlled. As a result of the regained awareness, flourishing links have been formed most notably between the behavioural ecologists and the psychologists interested in the experimental analysis of learning. In behavioural development, too, functionally inspired approaches have played a useful role in making sense of what otherwise seemed a hopelessly confused area. Asking what might be the current use of behaviour helps to distinguish juvenile specialisations from emerging adult behaviour and helps to understand the developmental scaffolding used in the assembly process. Functional assembly rules are important, for instance, in determining when an animal gathers crucial information from its environment. With attention focused on the problem, attempts can be made to analyse the mechanisms. Here again the optimal design approach frames and stimulates research on the processes of development (see Bateson 1987).

The stream of ideas between "how" and "why" approaches flows both ways. Finally and at last, many people who would call themselves sociobiologists or (more commonly these days) behavioural ecologists are beginning to appreciate the need for knowledge of the mechanisms to address the functional and evolutionary questions in which they are most interested. This has happened notably in the studies of perceptual factors and learning processes influencing mate choice and their implication for associated evolutionary theories of sexual selection. It is also happening in areas of work generally lumped under the heading of "life-history strategies", which raise important issues to do with conditional responses to environmental conditions. In general, these changes in thought are occurring because what animals actually do is being seen as important in stimulating (as well as constraining) ideas about the function and evolution (see Stamps 1991). The mechanisms involved in the development and control of behaviour may often feed back into evolutionary processes, as seems likely to have been the case with mate choice and with the active control of the social environment (see Bateson 1988).

While the barriers between the "why" and the "how" approaches have once again become more permeable, enormous strides had been made in neuroethology and in understanding the hormonal basis of behaviour. Links between the physiology of metabolism and behaviour were being made, as well as between behavioural state and the immune system. The relevance and value of molecular techniques was beginning to be realised. In general, studies of the development and control of behaviour look very different now from how they seemed twenty years ago.

Experimentalists are less likely these to hold all but one variable constant and when the single independent variable was found to produce an effect, it was *the* cause and everything else was deemed unimportant. A systems approach is essential and behavioural biologists are particularly well-equipped to provide it. Some of the most interesting people studying the neural basis of behaviour know only too well that the data they obtain are much the same as those obtained by a meteorologists in the middle of hurricane working at ground level. They have realised that if you want a coherent sense of the whole system you need the equivalent of a satellite picture. Only the people who study behaviour provide it for them.

In this dramatically changed environment the time seems right to rebuild an integrated approach to behavioural biology. With a whole array of promising new research areas emerging, behavioural biologists have a lot to be self-confident about. This matters in a highly competitive world in which determined and well-placed people can, in a remarkably short time, change what is and what is not funded, close research institutes and radically alter the departmental structure of universities. Whether or not a meeting like this can do anything as ambitious and portentous as drawing up a new agenda for behavioural biology remains to be seen. At the very least, though, it should offer to the new generation of young scientists who are coming into the field a sense of what are becoming the most exciting areas in the subject.

Further reading

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FORAGING

Combining function and mechanism in a model of herbivory

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The objective of my talk was to show how a technique from behavioural ecology, stochastic dynamic modelling, can be applied to the analysis of plant-herbivore interactions. The system selected for study was the behaviour of sheep grazing on mixtures of perennial ryegrass and white clover. This was chosen because of its economic importance in agriculture in temperate regions of the world. From the point of view of the farmer, the practical objective is to stock ryegrass-clover swards with sheep in such a way as to maintain the sward at an appropriate equilibrium mixture. The equilibrium mixture depends both on the intrinsic properties of the two plant species that determine their relative growth and competitive abilities and on the effects of grazing on the two species. Selective grazing, for example, would tend to reduce the cover of the preferred species.

Previous attempts in the agricultural literature to model and/or examine empirically both the total daily intake of sheep and their preference for grass or clover have produced inconclusive results. The daily intake of sheep appears to reach an asymptote below the limit expected from physiological constraints of intake, passage and absorption. The preference of sheep for ryegrass and clover appears to be changing and inconsistent: experimental studies are equally divided between those that conclude sheep prefer clover, those that conclude they prefer grass, and those that conclude sheep have no preference.

The stochastic dynamic model consisted of a behavioural repertoire (rest, ruminate, forage for clover, forage for grass); three state variables (indigestible material in gut, digestible material in gut, energy levels); stochastic elements (encounter with food, predation hazard); and fitness consequences (survival as a function of reserves, predation hazard associated with different activities). The technique of stochastic dynamic modelling allows one to determine the optimal (fitness maximising) trajectory of behaviours through a time period. The model requires detailed physiological information which was obtained from the agricultural literature, combined with estimates of the fitness consequences of behaviour. The dynamic aspect of the model arises from the fact that the internal state of the sheep changes in a dynamic way as a consequence of behaviour.

The model was able to account for the observed asymptote in daily intake of sheep below their physiological constraint. According to the model, this asymptote arises from the tradeoff between benefits of feeding and benefits of other activities such as vigilance. The model is also able to offer hypotheses to explain why preference for grass and clover is inconsistent: the model predicts that preference depends on relative abundance of the two species, on state of the sheep (energy requirements), and on time of day. These effects arise from the interaction between intake rate, passage rate, and absorption rate, which differ between the two species. The effect of time of day on preference (clover preferred in the morning, grass preferred in the afternoon) was tested in a field-scale experiment in which sheep were monitored continually by video cameras. The empirical results supported the predictions of the model.

This example shows how analysis of behavioural mechanisms can be enhanced and strengthened by incorporating functional considerations. It raises the question of whether a purely mechanistic model could, in principle, have explained the same results. Clearly, there has to be a set of mechanisms underlying behaviour. So in principle a mechanistic model could explain and predict the behaviour. Possibly the role of functional elements in the model was to provide a basis for understanding the decision processes without a complete analysis of the physiological mechanisms causing the decisions. However, it may be ultimately necessary to include some functional considerations in any model of mechanism, because the decision process is likely to involve calibration of the potential benefits derived from different behavioural options.

Acknowledgement

This work was funded by the United Kingdom Agricultural and Food Research Council. I thank Jonathan Newman, Tony Parsons and Peter Penning for permission to quote their unpublished data. The work is a joint project between the AFRC Unit of Ecology and Behaviour at Oxford University and the Institute of Grassland and Environmental Research at North Wyke, Devon.

MEMORY PROCESSES AND OPTIMAL FORAGING

Alejandro Kacelnik

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Optimal foraging models fail to predict actual behaviour at least as often as they succeed. These failures, I argue, are not drawbacks of the approach but rather useful stepping stones in a program of integration of mechanistic and functional explanations of biologically complex phenomena. Without this integration, evolutionary interpretations often fall into untestable speculation, while purely descriptive analysis of behaviour concentrates on sterile analysis of biologically meaningless properties of animal behaviour. As an example, I shall consider the algorithms involved in decision making by animals engaging in foraging tasks.

It is usually acknowledged by evolutionary biologists and behavioural ecologists that -everything else being equal- natural selection ought to favour individuals who are more efficient in gathering resources at a higher rate per unit of time (viz. Stephens & Krebs 1986). On this basis, a number of optimality models have been developed that predict the optimal choices of animals facing various behavioural alternatives, disregarding the cognitive processes involved in the control of behaviour. This can be illustrated with the controversy sparked by the identification of the so-called Fallacy of the Averages. In an article published in 1981, Templeton & Lawlor pointed out that in stochastic foraging problems including recurrent choices, the rate of energetic gain over the whole period under consideration ($\frac{\text{Expected Gain}}{\text{Expected Time}}$) is not the same as the average rate of gain per cycle of choice (Expected $\frac{\text{Gain}}{\text{Time}}$ per cycle). They correctly pointed out that previous theoretical models and the resulting research had been based on the first assumption, while claiming that in their view the relevant maximised currency ought to have been the second. Several authors quickly pointed out that this claim was in itself a fallacy (which was naturally called the Fallacy of the Fallacy of the Averages) because an animal maximising overall rate of gain ought to have higher reproductive success than one who maximised the per cycle rate at the expense of the overall rate. The logical strength of this reply appeared to settle the issue without recourse to empirical research. Now consider the following foraging situation. An animal faces a recurrent choice (in consecutive 'trials') between operating two food sources, identified as colours in simultaneously available pecking keys. Operating one of them (Fixed) results in a food reward after a certain delay from the time of choice. Choosing the alternative (Variable) results in food after either of two equiprobable delays, one shorter and one longer than the delay in the fixed option. The problem is schematically presented in figure 1.

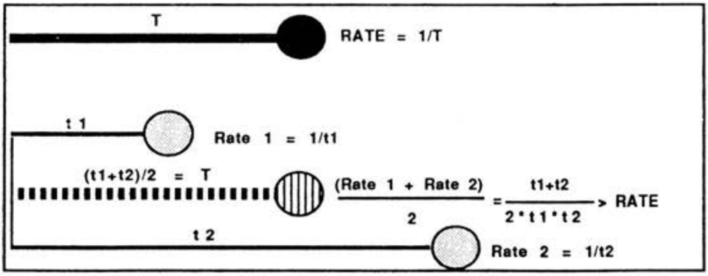

Figure 1

The horizontal lines represent waiting times from the moment of choice, and the circles the delivery of a food reward. The thick line followed by a solid black circle represents the fixed option, which leads to a waiting time T every time it is chosen. The two thin solid lines represent the variable food source, which leads to waiting times of either t1 or t2 with equal probability. The broken line between them shows a putative average representation of the two outcomes of the variable source. The figure illustrates the consequences of two forms of information processing. If the animals perceive and base choices on the waiting times, and t1 and t2 are programmed so that their mean equals T, then the two sources ought to be equally rewarding. This is to be expected according to the maximisation of $\frac{\text{Expected Gain}}{\text{Expected Time}}$, and is shown in the legends over the horizontal lines representing waiting times. If instead the subjects perceive rewards directly as gains devalued by the waiting times leading to them, i.e. as rates of gain, and store this information at the time of the reward, then they would be storing individual observations as ratios of $\frac{\text{Gain}}{\text{Time}}$, namely as observations of T^{-1} for the fixed option and either $t1^{-1}$ or $t2^{-1}$ for the variable option. The subjective rate of reward gains from the variable source would be equivalent to the mean of the reciprocals of t1 and t2, as shown on the right hand side of the scheme in figure 1. Under this form of representation, the variable source offers a higher subjective rate than the fixed one. In experiments based on this design, starlings (*Sturnus vulgaris*) strongly preferred the variable food source (Řeboreda & Kacelnik 1991, Bateson & Kacelnik in preparation).

We explored the problem in greater detail by means of a titration procedure that allowed for the identification of the value of fixed waiting time which led to indifference between the fixed and the variable option. We calculated the expected indifference value of the fixed source assuming that the two outcomes of the variable source were averaged globally or on a per-cycle basis and according to whether the inter-trial interval was included or not. The results for six experimental animals are shown in figure 2

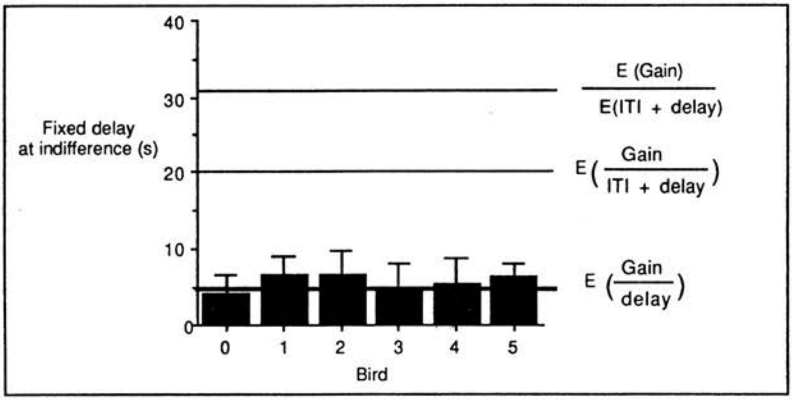

Figure 2

In the figure, E refers to mean values, delay is the interval elapsed between the point of choice and the reward delivery, ITI is the inter-trial interval and error bars are within-subject standard deviation. The horizontal bars show what would have been the indifference point if the subjects had used each of the given criteria for computing subjective values. The results show that the birds considered the fixed delay source to be equal in value to the variable delay source when the delay in the former equalled the harmonic mean of the two delays in the variable source, excluding the inter-trial interval. Both the averaging process (harmonic means rather than arithmetic means) and the exclusion of the inter-trial interval show that the choices did not maximise overall rate of gain. Instead, the subjects behaved as if they used directly perceived rates of gain and only paid attention to delays associated with each specific choice.

These findings have been paralleled in experiments based on different experimental designs, and indicate that a major revision of optimal foraging theory may be necessary once actual information-processing mechanisms are taken into account. My collaborators and I are working on two lines of analysis: we are examining the generality of the psychological mechanisms causing these preferences while simultaneously developing a theoretical account of the selective pressures which might have favoured these mechanisms over those leading to the maximisation of expected energy gains over total time.

Acknowledgement

I am very grateful to Melissa Bateson permission to quote her unpublished data.

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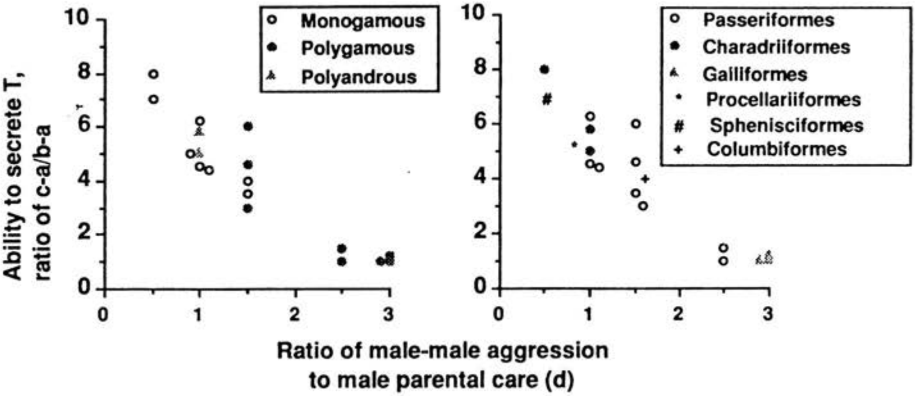
SEXUAL BEHAVIOUR

AGGRESSION, MATING SYSTEMS AND HORMONE-BEHAVIOR INTERACTIONS IN BIRDS.

J. C. Wingfield, Department of Zoology, NJ-15, University of Washington, Seattle, Washington 98195, U.S.A.

There is accumulating evidence that testosterone (T) secretion is correlated with expression of reproductive aggression, especially during social conflicts over dominance status, territories and mates. In more stable conditions after hierarchies have been established, territory boundaries and pair bonds formed, then correlations of circulating levels of testosterone and aggression are less obvious. These observations led to the "challenge hypothesis" suggesting that secretion of T may actually increase and sustain the frequency and intensity of aggression in reproductive contexts during periods of social instability. Measurements of plasma levels of T in free-living male birds confirm this relationship and also indicate that if males also show parental care then the level of circulating T tends to decrease dramatically since high levels apparently are incompatible with feeding of young. These data suggest further that behavioral interactions among males and females may have a direct effect of the control of T secretion in relation to complex social relationships including mating systems and breeding strategies. Patterns of T secretion generally match mating system. For example in polygynous species, circulating T levels in blood remain higher for longer periods than in monogamous species in which males feed young. Furthermore, if males of monogamous species are given sub-cutaneous implants of T to maintain high concentrations in plasma (i.e. similar to the pattern in polygynous species) then these males gain additional mates. This raises the question as to why polygyny is thus not more prevalent in avian species unless there is a cost to high sustained secretion of T. Field investigations revealed that high circulating T does not incur a cost in terms of stress or debilitation of energy reserves, but rather reduces reproductive success in males that normally provide parental care. In many polygynous species males provide little if any parental care and thus there are no restrictions on time spent in aggressive interactions with other males for territories and access to females. If males do show paternal care, then T levels must decline because high levels of male-male aggression and parental behavior are incompatible. This series of investigations on free-living birds led to the hypothesis that polygynous males have high and prolonged circulating levels of T in blood because social interactions among males and with sexually receptive females stimulate secretion of testosterone thus maintaining elevated concentrations. Monogamous males, on the other hand, may be less sensitive to social cues regulating T secretion resulting in lower levels, especially during the parental phase of the nesting cycle.

Experiments on the interrelationship of social interactions and secretion of T in male birds have, however, revealed conflicting results. In those species in which males provide substantial parental care (e.g. *Zonotrichia, Passer*), T inhibits expression of parental behavior. Circulating levels of T are low throughout the parental phase. However, if males are challenged, or when females once again become receptive, subsequent behavioral interactions result in an increase in T secretion to facilitate a high rate of territorial aggression and mate guarding. In contrast, those species tending toward polygyny and/or little male parental care (e.g. *Agelaius, Lagopus*), do not appear to respond to male-male interactions or exposure to receptive females with a rise in circulating T. Others (e.g. *Molothrus*), show intermediate responses. These relationships are revealed in Figure 1A. The ability to increase circulating levels of testosterone above the breeding baseline (**b**) corrected for the non-breeding baseline (**a**), to a maximum level (**c**) also corrected for the non-breeding baseline (i.e. the ratio of **c-a/b-a**) is plotted against an index of the degree of male-male aggression and parental care (**d**). It was expected that polygynous males which show little parental care and interact aggressively with other males throughout the season, should have a high responsiveness for social modulation of T secretion (i.e. high ratio of **c-a/b-a**). In Fig.1A it is clear that the reverse is true. Polygynous males tend to have a lower responsiveness of T secretion to social cues. These data indicate that males with low parental care and high male-male aggression may secrete T at a maximum rate throughout the season regardless of social stimuli, i.e. control of T secretion may be genetic rather than social. However, in monogamous males, or those species in which males show high parental care (note that 3 polygynous species overlap with monogamous males in Fig. 1A; all these males show high parental care), plasma levels of T must decline during the nesting phase so that parental behavior can be expressed fully. However, these males retain the ability to increase secretion of T when challenged by another male for territory or mate. In these species regulation of T secretion by social cues is well developed. Note also that these data suggest significant differences in neural pathways for environmental signals in relation to mating system.



There is also a phylogenetic component in this relationship (Fig. 1B). In many Charadriiformes males show parental care whereas in most Galliformes males do not and tend toward polygyny. Hence these groups of species tend to polarize in their relationships of **d** to **c-a/b-a**. Passerines, on the other hand, show great variability - a reflection of this extremely large and diverse group.

It is proposed that hormonal responsiveness to behavioral interactions is related to mating system and breeding strategy. Greatest responsiveness appears in males with most parental care and, perhaps paradoxically, least in males showing low parental care but high male-male aggression.

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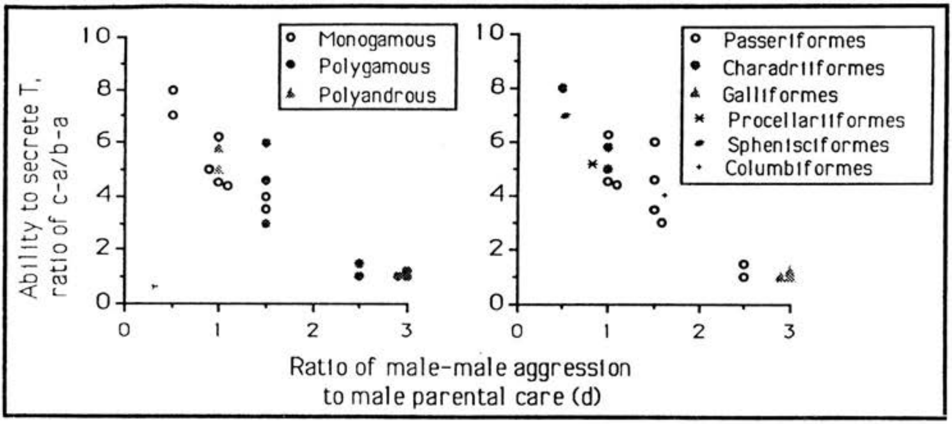

Ability to secrete T,
ratio of c-a/b-a
10
8
6
4
2
0
0
1
2
3
Monogamous
Polygamous
Polyandrous
Passeriformes
Charadriiformes
Galliformes
Procellariiformes
Sphenisciformes
Columbiformes
Ratio of male-male aggression
to male parental care (d)

Mechanisms of Mate Choice in Monogamy

by

George W. Barlow
Department of Integrative Biology and
Museum of Vertebrate Zoology
University of California, Berkeley

The Midas cichlid, *Cichlasoma citrinellum*, of Nicaragua is a biparental, monogamous fish. It is so isomorphic that the sexes can be distinguished by the observer only by examining their genital papillae. They reproduce over a wide range of sizes, but the female of pair is usually 70 to 90% the length of her mate. Pairs compete fiercely with other pairs for breeding sites, and most pairs are evicted from such sites before completing a reproductive cycle (McKaye & Barlow 1976, McKaye 1977). Consequently, both sexes are under intense selective pressures for high levels of aggression and prowess. That places the pair in a difficult situation, especially at the time of pair formation but also after pairing. Because the sexes look alike, each stimulates in attacking in the other, and much aggression-related behavior appears during pair formation. However, the pair must suppress attacking and cooperate to raise their offspring.

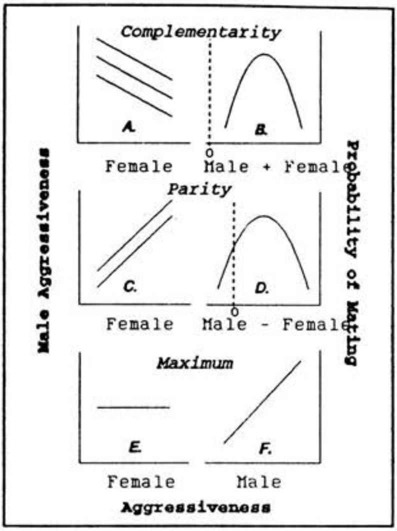
The Midas cichlid is also color polymorphic. Most adults are gray with dark markings and various amounts of red or orange on the throat and in the eyes; these are called normal morphs. About 8% of the adults, however, lack melanin in their skin and are colored yellow through orange and are labeled gold morphs. Golds and normals are equally aggressive, given much individual varition, but when all else is equal, golds dominate normals. The gold color appears to inhibit aggression in the other fish. This may have repercussions for pair formation.

In the field, most pairs mate assortatively by color (McKaye & Barlow 1976). In the lab, fish that are free to interact also mate mostly assortatively (Barlow & Rogers 1978). However, when females chose mates through a one-way mirror, precluding interaction, they showed a weak but significant preference for normal males, irrespective of their own color or experience (Barlow *et al.* 1990). Males did not discriminate among the females.

When females were offered a choice through a one-way mirror of males that differed either in size or in aggressiveness, they chose the larger and the more aggressive males, respectively (Rogers & Barlow 1991). Not surprisingly, larger males proved more effective in defending breeding territories than did smaller ones. And the more aggressive males, irrespective of their size, more successfully defended their offspring against small predators.

Again, males did not discriminate among females on the basis of size or aggressiveness. Should they have? Larger females are more fecund and are better able to defend the territory against interlopers. Perhaps the male can only assess the aggressiveness and prowess of the female through interaction, which the one-way mirror precluded in this experiment.

These results inspired three models to test further (Barlow 1992). The critical dependent variable is the probability of successful pairing; in an experiment, this was judged by the sum of male and female courtship. One model is *Most Aggressive*, shown at the bottom of the accompanying figure for females and males courting more as the males become more



aggressive. (It could also have been presented as courtship increasing as a function of female aggressiveness.) Empirical data suggest this model applies to females when they are safe from male attack, as when behind a screen of some type.

The second model is *Complementarity.* It derives from the argument that if both the male and female are highly aggressive they cannot pair, and if both are too unaggressive they cannot defend a territory. It predicts that courtship is maximized at some optimal *sum* of male and female aggressiveness. The result is an inverted-U curve.

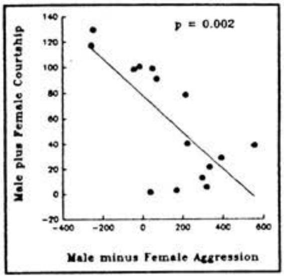
The third model, *Parity,* derives from impressions of courtship, that the male is usually more aggressive than the female; this might result from the division of labor of the pair: the male invests more in territorial defense, the female in protection of the young. This model predicts that combined courtship will peak at some optimal *difference* in courtship. Again, the result is an inverted -U curve.

Females were exposed to two males of about the same size but differing in aggressiveness, and tested twice with them. The first time, the female viewed the males through a large-mesh screen that permitted interaction, even biting if both fish pushed into the screen. The second test, on the following day, was done with the screen removed (the female could enter and depart the chamber through a slit large enough for her but too small for the male). The object was to see whether the female could mate with the preferred male when not protected by the screen.

Three independent variables were used. The critical one was aggressiveness of the three fish. I must stress that aggressiveness was measured *before* the observations of the fish interacting because two fish might be highly aggressive but compatible, in which case little aggression would be observed between them. Each fish was exposed to its mirror image and attacks were tallied. The other independent variables were relative size of the female and female gonopodial papilla (FGP). We meant to keep female relative size constant, but limitations of fish available resulted in some variation. FGP also varied; the larger its size, the closer the female was to spawning.

As in the previous experiment (Rogers & Barlow 1991), females spent more time with the more aggressive males with the screens in place, though the result was not significant (the experiment is in progress). Choice was obvious — the female stayed almost exclusively with one male or the other. When the barrier was removed 43% of the females either could not or did not mate with the previously chosen male; some left his compartment and some remained, though courtship fell to zero in the latter case and aggression was frequent. Of those females, 29% switched to the male they had previously ignored. Thus in nearly half of the trials, pairing was unsuccessful with the "preferred" male (some of the females could not, or would not, mate with the other male).

The *Complementarity Hypothesis* was examined in a scattergram, with total courtship plotted as a function of the sum of aggression. No pattern was apparent, certainly not an inverted U-curve.



The *Parity Hypothesis* was also rejected. The sum of male and female courtship, as a function of the difference in aggression, did not plot as an inverted U. However, a distinct linear relationship emerged, shown in the adjacent figure. The more female aggression exceeded male aggression, the more the two fish courted.

Perhaps this relationship could be explained as a result of more aggressive females being more attractive. Apparently not. Male courtship regressed on female aggression had a negative slope and was only just significant (p = 0.054). Male courtship was also correlated positively with FGP (p = 0.003). Relative size of female produced a robust outcome: The larger the female the more total courtship was seen (p = 0.017).

To assess the relative contributions of the three independent variables, I performed a stepwise regression to find the best predictors. Difference in aggressiveness was the best one (p = 0.030). Relative size of female was the next best predictor (p = 0.035) but it fell out in a backward-step analysis. FGP failed to predict.

If progress in science is made by rejecting hypotheses, this study was a success because all three basic hypotheses were rejected. The results, nonetheless, were informative. Testing the hypothesis of *Most Aggressive* male revealed a provocative conflict between behavioral mechanisms: Females were often unable to pair with the mate of choice.

The results also indicated a possible conflict of interest between the sexes, even though they have identical fitness after pairing. Males should prefer large females, and indeed relatively large females produced more courtship in both mates. This could mean, further, that males need interaction in order to choose a mate. Females should prefer relatively unaggressive males, judging from the courtship of pairs in which females were much the more aggressive sex. However, when choosing a male behind a barrier, females consistently selected the largest and most aggressive males available.

This experiment will be extended to consider the fitness of pairs that are picked for differing relationships in their aggressiveness. Such pairs will be allowed to breed in a pond in the presence of predators on their young.

These results indicate that it is necessary to understand the behavioral mechanisms underlying mate choice if one is to interpret properly the outcome of experiments on choice, particularly for biparental monogamous species. They also reveal why one should be prudent in extending findings to radically different field situation. That the Midas cichlid mates assortatively in the field has been used as evidence to support the sexual-selection hypothesis for the explosive speciation of mouthbrooding cichlids in African rift lakes (McKaye 1980).

That hypothesis requires the active choice by females of males by color. However, assortative mating in the Midas cichlid apparently results from the indirect effect of color on aggression, and certainly not from active choice, as the hypothesis demands. Further, so far no evidence has been provided that the African cichlids select mates on the basis of color.

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Functional and causal aspects of sperm competition in birds.

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Sperm competition is widespread in the animal kingdom, and occurs regularly among birds despite their mating system being predominantly mongamous. Sperm competition occurs when females copulate with two or more males during a single reproductive cycle. Behavioural ecologists have asked why females of socially monogamous species should form a pair bond with one species only to copulate later with another male. The answer seems to be that this is one of several different ways in which females can modify their their initial mate choice and thus have their eggs fertilized by particular males (Møller 1992; Birkhead & Møller 1992). Other ways in which females can influence who fathers their offspring include behavioural means, and anatomical and physiological mechanisms.

There appear to be two main sperm competition mechanisms in the animal kingdom (Birkhead & Hunter 1990): (1) last male sperm precedence - in which the last male to inseminate the female fertilizes the majority of eggs, and (2) the raffle principle - where fertilization probability depends upon the relative numbers of sperm from different males. Both these mechanisms operate in birds, but on different time scales. When copulations occur close together in time a raffle operates, but when the copulations are well-spaced the mechanism is last male sperm precedence (Birkhead & Møller 1992).

The mechanism which results in last male sperm precedence is not known. Poultry biologists favour the stratification hypothesis, where the sperm from successive ejaculates remain stratified, or layered within the female's sperm stores. However, Lessells & Birkhead (1990) modelled this and found that stratification could not account for the observed levels of precedence. Instead, sperm displacement - where incoming sperm displaced those already present, was much more plausible. Some empirical observations also support the displacement hypothesis.

Females might attempt to control the paternity of their offspring through (i) behaviour, (ii) sperm storage and utilization and (iii) through sperm selection.

(i) If females control copulations, as they appear to do in most species, then by terminating copulation before the end of their fertile period and by performing an extra-pair copulation with a more preferred male, females would have the opportunity to determine the paternity of their offspring.

(ii) Following copulation, females might selectively destroy or eject sperm from less preferred males, in favour of those from a more preferred individual.

(iii) Following copulation the reduction in sperm numbers in successive segments of the female reproductive tract is dramatic: from several million to less than one hundred. This intense selection is brought about by a series of chemical, physical and immunological barriers in the female reproductive tract, and provides the opportunity for females to select sperm. There is no empirical evidence for such selection at present, but several lines of circumstantial are consistent with this hypothesis. This idea rests on the assumption that a correlation exists between sperm quality and offspring quality. Traditionally this has not been thought likely, but it is possible that some linkage exists between a sperm's characteristics and its genotype (Birkhead et al. in press).

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SPERM COMPETITION AND FEMALE SELECTION IN MAMMALS: WHY MECHANISMS MAKE ALL THE DIFFERENCE

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Female choosiness and male-male competition do not end when mating takes place. After mating, ejaculates face considerable barriers within the female reproductive tract and, when more than one male copulates with a female, sperm from rival males will compete within the female tract to fertilize the ova that are available.

In order to understand how different individuals achieve their reproductive success we have to take into account the physiological mechanisms that come into play after mating. By incorporating the study of these mechanisms we may also improve our understanding of sexual behaviour and even of mating systems. On the other hand, the functional approach has the potential of integrating new findings in reproductive biology which so far have not been examined from an evolutionary perspective.

Mammalian reproductive biology differs in crucial respects from other better-studied groups such as birds and insects (for recent reviews see Roldan et al. 1992, Gomendio & Roldan 1993). Female mammals do not posses proper sperm storage organs (such as the sperm storage tubules and spermathecas present in birds and insects respectively), and as a consequence mammalian sperm live for short periods of time once ejaculated into the female tract (bats being a well known exception). Female mammals are sexually receptive for limited periods of time within each sexual cycle (i.e. oestrus), and ovulation time is relatively unpredictable. Once ejaculated, sperm are transported passively by movements of the female tract but must also swim actively to go through certain physical barriers such as the cervix and the uterotubal junction. Those sperm that get through the uterotubal junction spend a short period of time in the lower isthmus of the oviduct. During this short period of residence only sperm which associate with the oviductal epithelial cells are able to survive. After ovulation takes place, sperm swim actively towards the ova, and once in the vicinity of the ova sperm release the enzimes contained in the acrosome, penetrate the ova vestments and fertilization takes place. Mammalian sperm are unique in that they need to become "capacitated" before they can fertilize the ova.

Sperm competition has selected for an increase in the number of sperm that a male deposits in the female tract (Parker 1984). This increase may be achieved by increasing the number of copulations, and/or by increasing the number of sperm in each ejaculate (Ginsberg & Huck 1989). The latter has been achieved mainly by an increase in relative testes size (Harcourt et al. 1981, Kenagy & Trombulak 1986). For some time, it was assumed that there was a trade-off between sperm numbers and sperm size, and thus that the increase in sperm numbers under sperm competition had been achieved at the expense of a reduction in sperm size. Contrary to this prediction, sperm are longer in species confronting sperm competition than in monandrous species (Gomendio & Roldan 1991). Sperm competition seems to have favoured the evolution of longer sperm, because these are able to swim faster and will thus outcompete sperm from rival males in the race to fertilize the ova.

In birds and insects the last male to copulate with a female will be more successful at fertilizing the ova (Parker 1984, Birkhead & Møller 1992) In mammals there are no such order effects and it is the male who copulates closest to the time of ovulation that will be more successful at fertilizing the eggs. In birds the combination of last male advantage on the one hand, and sequential ovulation and fertilization of the eggs on the other, may have led to the evolution of pair bonds and even contributed to the evolution of paternal care. By contrast, in mammals there are no order effects and, within each sexual cycle, all the ova are ovulated and fertilized simultaneously. Thus, whether a male does any mate guarding will depend on a number of factors such as the degree of synchrony between the females in the population, the length of oestrus, and the predictability of ovulation. Under these circumstances, pair bonds and paternal care are unlikely to evolve.

Female selection has so far received little attention as a selective force shaping ejaculate features (reviewed in Roldan et al. 1992). In mammals, ejaculates face considerable barriers within the female reproductive tract and these may represent a form of female choice to some extent. We have considered three different constraints that a female may impose on male ejaculates. (1) *Temporal constraints*. When females are in oestrus for longer than sperm are able to survive, males face the risk that their sperm may be unable to fertilize by the time ovulation takes place. There is a positive relationship between oestrus duration and sperm fertile life, which is even stronger when the period of time between the beginning of oestrus and ovulation is considered instead. This may have been achieved partly by changes in sperm size because short sperm have longer life-spans than long sperm. Thus, when oestrus is long males produce short sperm which will survive for longer.

Conversely, when females are in oestrus for short periods, males produce long sperm which will not survive for long but will capacitate more quickly, and will thus be ready to fertilize when ovulation takes place. (2) *Spatial constraints*. When sperm have to swim long distances males produce short sperm which will survive for longer and are also less susceptible to damage. It may also be advantageous to produce long sperm when the distance to cover is short, because under sperm competition the most efficient strategy may be to swim fast when the distance is short and more slowly when the distance is long. (3) *Thickness of the ova vestments*. Because in mammals the ova vestments are particularly thick, we expected to find a positive relationship between the thickness of the ova vestments and sperm length. However, no relationship could be found.

At present there is not enough information available to combine the relationships found between female traits and sperm size with the findings regarding sperm size and sperm competition. We will have to await until there is information on both selective pressures for the same sample of species before we can carry out such an analyses.

Given the magnitude of these female barriers it is worth asking why they have evolved. There are a number of possible answers which include: (a) female barriers are the result of other selective forces, (b) have evolved primarily to prevent infections, (c) have evolved to prevent polispermy, (d) they enable the selection of sperm within an ejaculate, and (e) they enable the selection of spermatozoa from different males.

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SIGNALLING

Honest Signalling. **J. Maynard Smith**

An "honest" signal is one that conveys accurate information about the state, genetic or motivational, of the signaller: a "costly" signal is one that reduces the fitness of the signaller more than is necessary to transmit the required information unambiguously. Zahavi (1977, 1981) has argued that signals can be honest only if they are costly - essentially because cost-free signalling systems are open to invasion by liars - that is, individuals that signal that they are in a certain state when in fact they are not. Enquist (1985) showed, in a formal model of a contest between two individuals over a resource, that it can be evolutionarily stable to send a risky signal if, and only if, the sender has a particularly high need for the resource. Grafen (1990) developed a more general game theoretic model of honest signalling, which essentially confirmed Zahavi's original assertion: although formulated in the context of sexual selection, his model has a more general relevance.

The Philip Sidney game (Maynard Smith, 1991) is an attempt to capture the essence of the argument in a simpler and more accessible form. To achieve mathematical simplicity, the cost of a signal, and the fitness outcomes to the participants, are treated as discrete and not as continuous variables. The model confirms Grafen's finding that there are situations in which signals must be costly if they are to be honest. However, the discrete nature of the model leads also to the conclusion that there are situations in which cost-free signals can be honest. This will be the case if the signaller and receiver would place the possible outcomes of the interaction in the same rank order, in fitness terms: it is not necessary that the strengths of their preferences should be the same. This raises the question of whether situations allowing cost-free signalling arise frequently, or at all, in the real world.

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Sensory Systems, Signals, and Signalling Behaviour

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Signals are disturbances in the environment caused by one organism (sender) which convey information to the receiver. The reception of the information must be clear enough to allow the receiver to make a behavioural decision. Two components of signals evolve: (i) information *content*, or what is being transmitted: and (ii) signal *design*, or the form required for efficient emission, transmission, reception, and recognition. There has been much theoretical work done on the evolution of signal content, especially with respect to sexual selection and honest signalling (*e.g.* Grafen 1990), but very little on the physical design of signals (Endler 1992). Any consideration of the evolution of signals must consider how the signal is generated and emitted, how it fares during transmission through air or water, how it is received and processed by the receivers's sensory systems, and the factors which affect the value of alternative ways of reacting to the information contained in the signal. Some of the factors are summarized in this table:

SIGNAL GENERATION	TRANSMISSION IN AIR/WATER	SIGNAL RECEPTION	REACTION CHOICE
Biophysical limits to form and intensity	Background noise	Sensory adaptive state (light adaptation, *etc.*)	Other signals
Energetic limits	Interfereing signals	Physiological state	Choice time wasted
Biochemical limits	Attenuation	Attentiveness	Reasons for choice
Energy storage	Blocking	Need to be attentive	Need for choice
Timing and location: predation short season correct place & time	Absorbtion	Need for alerting signals	Physiological state (hunger, thirst, etc.)
Information content *versus* clarity	Reflection & refraction	Short reception time	Predator risk
Information density	Distance	Other conspecifics	Parasite risk
Temperature (pheromones)	Spectral properties	Jamming	Quality of signal
	Self-interference	Signal reception rate	Reliability of signal
	Information density	Information processing rate	Signals different: individual or environmental variation
	Temperature (olfaction)	Noise	
		Temperature	

A careful consideration of each factor relevant for a particular sensory mode allows us to predict the form of signals for a given species signalling at a particular time, place, and micrometeorological conditions, and may also allow us to predict the outcome of choices made in response to the signals (Endler 1992). Some rules common to all sensory modes include: (1) redundant or repeating signal structure allows averageing-out of background noise; (2) greater amplitude and directionality makes transmission and reception more efficient; (3) higher frequencies are better if a high information transmission rate is required; there is less degradation by turbulence and faster response of receptors at higher frequencies; (4) species-specific and tuned receptors minimize the effects of noise at other frequencies; the use of paired receptors (one offset from the signal tuning peak) is an even more effecient way to reduce noise; (5) specific frequency bands, places, seasons, and times of day are associated with less noise, less interference from other species, and lower predator or parasite risks; (6) avoid signalling at same time as immediate neighbors (unless jamming is desired); (7) rapidly degrading signals are useful for short distance communication, especially when predators sense from longer distances; (8) simpler, more effective alerting signals should be used to attact the receiver's attention before sending the main (information-laden) signal. There are other predictions which are specific to each sensory mode (Endler 1992).

It is essential to consider both design and content when investigating the evolution and function of signals (all four columns in the table). For example, a consideration of only the content of a signal may predict one behavioural choice, but an additional consideration of some of the physical factors affecting the signal may yield a very different prediction about the choice.

The factors in the first three columns will be common to all species living and signalling in the same conditions, so we can predict that some properties of signals should be predictable and common to such groups of species. Unlike the more general predictions (independent of habitat and sensory mode) of the fourth column, the predictions arising from the first three columns will be much more specific to particular species (although not necessarily restricted to the same taxonomic groups), so there will be a trade-off between generality and specific predictive power when one considers various aspects of the evolution and function of signals, sensory systems, and signalling behaviour. However, there is essentially no research which simultaneously tries to tie all four columns together in a single organism. Past research has either considered only column 4 and ignored the first three, or *vice versa*. It is time for a broader approach.

Because there are different suites of factors affecting the different sensory modes, it may in principle be possible to predict which sensory modes should be used for signals containing information of a particular level of complexity, and transmitted at a particular time and place. But once again, there has been essentially no research in this area.

The basic questions we should always ask when studying the evolution and function of signals are: (1) What information is being transmitted? (2) Which sensory mode (or modes) is used for most of the information transmitted? (3) When, where, and under what environmental conditions is the signal transmitted? (4) What are the intended and unintended receivers? (5) How does the interplay between the environment, signal properties, receiver properties, and signal content affect the function and evolution of the signal? (6) How does this affect behaviour, which presumably chooses times, places and modes which are most effective in reaching the receiver, avoiding unintended receivers, and giving the desired information to the receiver? (7) What biophysical propreties favor particular signals and associated behaviour? (8) What sensory properties favour particular signal designs and signalling behaviour? (9) How does the tradeoff between efficiency and content affect signal design and signalling behaviour? (10) How is the tradeoff between successful signalling to conspecifics and inadvertant signalling to predators or parasites accomplished, and can advantage be taken of varying sensory properties and modes? (11) How much do these tradeoffs influence each other and signalling behaviour? (12) How much do these factors influence the evolution of sensory systems and which sensory modes are used to transmit information? Answers to these questions would be fascinating and valuable.

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Receiver psychology and the design of warning signals

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Recent analyses of the evolution of biological signals give the impression that signalling systems are either governed by handicap selection for honest advertising, or are the product of sensory exploitation. I argue, however, that signals are designed both by the characteristics of the message they convey ("strategy"), and by the need to convey that message effectively ("efficacy"). I illustrate these concepts with reference to warning signalling systems, concentrating particularly on the role of signal efficacy. Although signal efficacy has been studied before, particularly in terms of efficiency at transmission through different environments (e.g. Lythgoe 1979), or efficiency at keying in to receiver sensory sensitivities (Endler 1992), the role of "receiver psychology", and particularly the mechanisms of learning, has been neglected (Guilford & Dawkins 1991). I illustrate how the functional design of warning signals is closely related to the mechanisms of predator learning by presenting the results of a recent study on the role of aggregation in aposematic prey (Gagliardo & Guilford 1992). In this experiment, 38 naive domestic chicks (*Gallus gallus domesticus*) were pre-trained to walk singly down an open topped 5m long run-way to obtain food items (sieved chick starter crumbs, dyed with food colouring) from a series of sunken wells. Once pre-trained, chicks were placed in one of four treatment groups for the rest of the experiment, where each treatment offered palatable prey (dyed green) and unpalatable prey (dyed yellow, and tainted with quinine hydrochloride) in a different arrangement. Birds learned to discriminate green from yellow crumbs over a series of 20 trials, and were then subjected to a further 10 extinction trials in which both crumb colours were made palatable. Discrimination performance under the four treatments is illustrated in Figure 1. When crumbs were arranged in aggregations (Aggregated treatment) birds learned to avoid them faster, and for longer under extinction, eating fewer in the process than when crumbs were arranged solitarily in each well (Single treatment). Prey aggregation clearly enhances warning signal function. In the next treatment prey were offered solitarily, but were placed on top of a perspex window in each well underneath which were inaccessible aggregations of crumbs (Visually Aggregated treatment). Thus, in the Visually Aggregated treatment, prey appeared to be part of an aggregation but could only be ingested singly, yet learning was again significantly more effective than in the Single treatment and indistinguishable from the Aggregated treatment. From this it is clear that the enhancing effect of aggregation is visual rather than ingestive. Most surprising, though, was the fact that the same enhancement was also achieved in the fourth treatment, the Visual Single treatment. Under the Visual Single treatment, crumbs were available solitarily, but appeared on top of a second inaccessible crumb that became visible after the accessible crumb was removed by the chick. This indicated that the aggregated pattern of prey is not essential for the enhanced learning effect. We suggest that this is in fact caused by the temporal contiguity of visual stimulus and punishment generated by having similar prey still visible during, or immediately after, perception of the quinine itself. If this hypothesis is correct, then it suggests that aggregation in aposematic prey may have evolved to exploit the rules of learning in predators to enhance warning signal function. We are currently investigating further ways in which receiver psychology may have affected the evolution of signal design for efficacy.

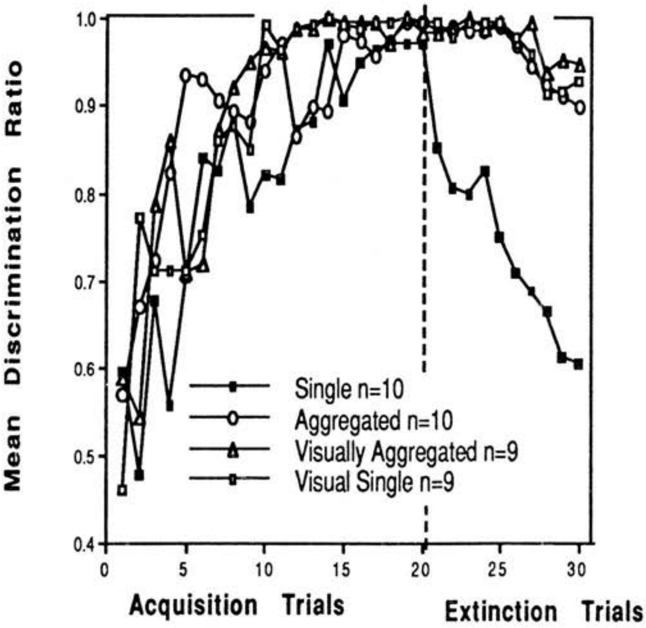

Figure 1. Mean discrimination performance during Acquisition trials, when yellow crumbs are unpalatable, and Extinction trials, when they are switched to being palatable (indicated

by the dashed line), for each of the 4 experimental treatments. Performance is measured as discrimination ratio (green crumbs attacked/ yellow + green crumbs attacked), which reflects the degree to which birds avoid yellow crumbs selectively (1=perfect discrimination; 0.5=no discrimination). Statistical significance of treatment differences are given in Gagliardo & Guilford (1992).

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PARENT-OFFSPRING RELATIONSHIPS

G. A. PARKER

Parent-offspring conflict: the relevance of mechanisms for modelling

Since the initial controversy as to whether or not it could exist, there have been a series of models of parent-offspring conflict. These have in general confirmed Trivers (1974) prediction that an evolutionary conflict of interests can exist between a parent and its offspring over the amount of parental investment. However, although a potential conflict exists, we can be much less certain about how this conflict is likely to be resolved. The various models make very different predictions about ESS outcomes: that is, how much parental investment is likely to be given, how much each offspring is likely to get, and what sort of costs will be involved in gaining parental investment.

I review very briefly the assumptions and predictions of three types of model for sib-competition and parent-offspring conflict: dominance hierarchy models (Parker, Mock & Lamey 1987); 'pro rata payment' begging models (Parker & Macnair - various dates); and 'honest signal' begging models (Godfray 1991). The models differ quite radically in their assumptions about:
(i) behavioural mechanisms by which offspring compete over food input from the parent;
(ii) mechanisms by which parents allocate food to the offspring.
Until we know the exact mechanisms of sib-competition and the behavioural rules by which parents allocate food to offspring, it will not be possible to predict how parent-offspring conflict will be resolved in a given system.

This is very much a case where future progress is likely to depend on advances in our understanding of mechanisms.

Parent-offspring conflict: can we decide between models of signalling need and manipulation? Fritz Trillmich, Dept. of Behavioral Ecology, University of Bielefeld, PO Box 10 01 31, D-4800 Bielefeld, Germany.

According to Trivers (1974), conflict is expected between parent(s) and offspring about parental investment. However, the form of cost and benefit curves has never been measured exactly and is critical to the arguments about parent-offspring conflict. Graphical arguments are dangerous since benefit curves can just as easily be constructed which predict no or only minor parent-offspring conflict instead of major conflict (Fig. 1). Therefore, parent-offspring conflict should not automatically be assumed to influence all parent-offspring interactions.

It is a problem to infer the existence of genetic parent-offspring conflict in a given instance from the observation of phenotypic conflict (Mock & Forbes 1992 in press). The actual measurement of costs and benefits is complex and needs to be taken more seriously as a few examples show. Even apparently obvious assumptions may prove wrong, e.g. a positive correlation between time sucking and milk intake of young mammals.

Usually, intense signalling between parent and offspring has been taken to indicate conflict. However, this is not necessarily true. Weaning (phenotypic) 'conflicts' may also be interpreted as exchange of information about costs and benefits of the alternatives 'dependence' versus 'independence' to offspring and parent alike. Screaming and throwing tantrums by young and 'meanness' by parents may be interpreted as handicaps, i.e. costly signalling to ensure reliability of the information exchanged between parent and offspring (Godfray 1991). Exchange of reliable information can be in the interest of both parties, given that environmental (e.g. feeding) conditions vary more or less unpredictably, and that parents as well as young do not have full information about each other's state and foraging opportunities and abilities. Since high fitness values (survival of young, survival and future fertility of the parent) are at stake, interactants need to ensure accurate information transmission. Such costly signals can certainly in most cases best be understood as a sign of underlying parent-offspring conflict, since without the potential for conflict no highly costly signalling should evolve. However, to judge the actual (energetic, riskiness or time) costs of signals, these must be measured empirically to determine if they are higher than would be expected if reliable signal transmission were their only function. If parents are e.g. energetically limited it may prove that young correctly signal their need which, however, parents cannot fulfill, due to energetic constraints. Such a situation would produce the appearance of parent-offspring conflict when in reality the environment is constraining the options of parents. Also, we need to consider a much more active interest of offspring in weaning once the foraging alternatives of the juveniles have developed. Such a situation may exist in the northern fur seal where about 75% of all young wean themselves.

Developmental studies of the foraging abilities of juveniles are needed to enhance our understanding of their options, and to improve the interpretation of 'weaning conflict' and parent-offspring conflict in general.

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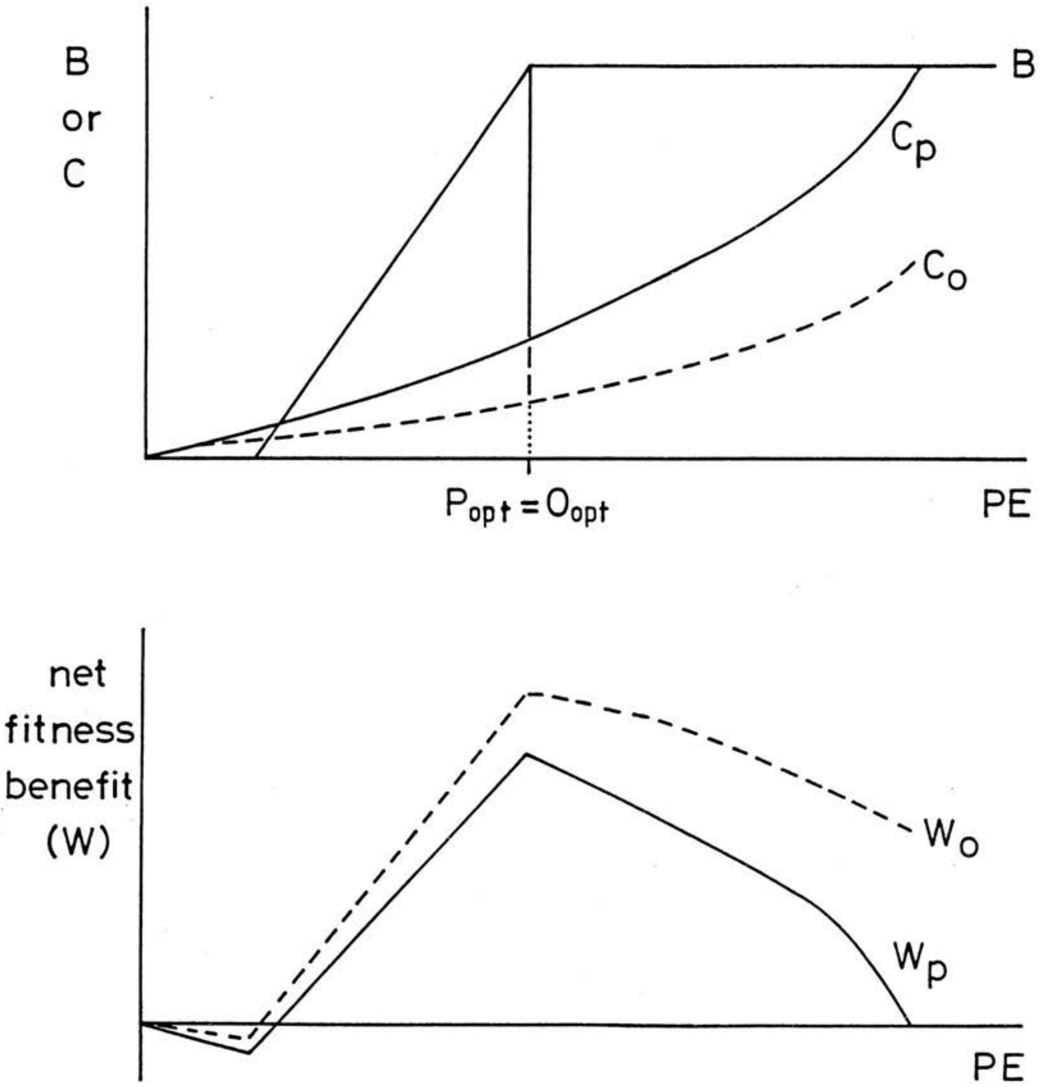
Trivers RL 1974. Amer. Zool. **14:** 249-264

Figure legend:

Potential benefit curve which produces no parent-offspring conflict. C = cost; B = Benefit; PE = parental expenditure. P_{opt} and O_{opt} designate parental and juvenile optima, respectively.


B
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The Design of Chick-Feeding Rules and How Cuckoos Can Exploit Them

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I discuss two examples of chick-provisioning by birds where a knowledge of mechanism is important for our understanding of adaptation.

The first is "helping at the nest". In many bird species the helpers are previous offspring of the breeders who remain at home because the habitat is saturated and there are no vacant breeding territories. By helping to raise their younger siblings the helpers increase their indirect fitness. The traditional behavioural ecology view of helping, therefore, is that "genes for helping" have been favoured by kin selection. Recently, Jamieson and Craig have challenged this view.[1] They propose instead that individuals are equipped with crude provisioning rules such as "feed any begging chick in my territory". When the habitat is full and juveniles are forced to remain at home, the presence of begging nestlings elicits provisioning. According to them, "helping" is not a trait but simply a by-product of a rule favoured in the context of parental care.

The key question to ask to distinguish these two hypotheses is "is not helping an alternative, or do individuals always blindly follow a crude provisioning rule? "Understanding the mechanism will tell us whether we should be measuring the costs and benefits of provisioning or of helping. Several recent studied have shown that individuals do not follow crude provisioning rules but rather vary their provisioning in relation to prospects of fitness gain. For example, white-fronted bee-eaters prefer to help close kin rather than more distant kin and if they have no close kin nearby they do not help.[2] In acorn woodpeckers, where two related males may share a female, experiments have shown that a male may sometimes help to feed the chicks even if he has no chance of paternity.[3] By contrast, in dunnocks, where two unrelated males may share a female, a male helps only if he has mated with the female.[4]

In dunnocks males do not discriminate in favour of their own sired young but follow a simple rule "feed the chicks provided I gained some matings with their mother". Why do males not have a more precise mechanism, such as some equivalent of DNA fingerprinting? Some social insects, like honeybees, and some mammals, like ground squirrels, can discriminate close versus more distant kin even when these are raised together in the same nest, perhaps by using phenotype matching - comparing their own odour label with that of their kin to measure relatedness. Birds do not have the array of odour cues available to insects and mammals and phenotype matching based on visual or vocal cues may be more difficult given that chicks change so markedly during development. So maybe birds are forced by constraints to use indirect cues to parenthood. Alternatively, direct markers may be possible but they may not spread because of conflicts of interest. For example, it would pay both mother and chicks to suppress paternity markers in cases where males would give reduced help or commit infanticide of young which are not their own.[4] A genetic model is needed here.

My second example concerns brood parasites. The inability of parent birds to "fingerprint" their young opens the way to their exploitation by cuckoos and cowbirds. Some hosts reject eggs which are unlike their own in colouration. How do they know which is the parasitic egg? Experiments show that hosts do not simply follow the rule "reject the odd egg" but can reject parasite eggs even when these form the majority of the clutch. Thus they know what their own eggs look like. Other experiments reveal that they learn their own egg-type in an imprinting-like process.[5] Several studies show that hosts are sensitive to recognition errors and vary their tolerance of deviant eggs in relation to the degree of mimicry of their own type, by the parasite.[6]

The study of learning mechanisms and rejection thresholds by hosts may provide a nice model system for studying how behavioural mechanisms change during evolution because different parasite-host systems are likely to be at different stages of a continuing evolutionary arms race.[7]

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Exploitation of host parental rules by brood-parasitic chicks

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Brood parasites and their hosts are thought to engage in a coevolutionary arms race where parasitism selects for adaptive defenses in the host (e.g. rejection of eggs unlike their own) which in turn select for counter-adaptations in the parasite (e.g. egg mimicry). Several studies suggest that mimicry in cuckoo eggs has evolved in response to egg discrimination by hosts. However, most brood parasites have not evolved chick mimicry and even those species of hosts capable of subtle discrimination against mimetic eggs appear unable to discriminate against a chick which looks strikingly different from the host chicks. So far, no satisfactory explanation has been found for this puzzling difference in host behaviour.

In the absence of parasitism, hosts seem capable of some discriminative processes between chicks within the same brood by following some simple rules, e.g. favouring the chicks in greater need of food or the larger chicks in asynchronously hatched broods. Since they are unrelated to hosts, brood parasites (and in particular cuckoos) may have evolved traits which exaggerate those favoured by hosts to care for their own offspring in the absence of parasitism (like deceptive persitent begging, fast growth rates and a large size relative to that of the host chicks) at no inclusive fitness cost. Here I suggest that such traits may prevent the evolution of chick discrimination rules by hosts if the probability of being parasitized is, as usual, low.

Hosts could evolve effective discrimination rules against the parasite by two possible ways. One is by modyfing an already existing rule like that of favouring the hungrier and larger chicks (e.g. "feed less the chick who begs more when it is the largest in the brood"). However, such modifications may be selectively disadvantageous in the absence of parasitism. A second possible way is by evolving a totally novel discrimination rule (e.g. "refuse to feed a chick of a different colour"). This is more improbable, as it may require a cumulation of coadapted mutations and may incur important rejection costs (mistakingly ejecting host chicks).

However, most cuckoo hosts can recognize the adult parasite and there is evidence that hosts caring for a fledgling cuckoo attack it when the cuckoo flies but ressume feeding it as soon as it stops and begs for food. This suggests that hosts are capable of recognizing the parasite at least during the fledgling stages. I postulate that the decision-making mechanisms in hosts involved in chick care are shaped in a way such that caring for a chick and discriminating against it are mutually exclusive states within a continuous motivational space, so that the more willing a parent bird is to favour a chick the less willing is to discriminate against it. The intense parental responses elicited by the cuckoo's exaggeration of such stimuli as intense begging and a large relative size, are likely to overwhelm any discriminative response in hosts triggered by the odd physical appearance of the parasite.

PARENTAL BEHAVIOUR

THE EVOLUTION OF LITTER SIZE IN MAMMALS: PROXIMAL AND FUNCTIONAL CONSTRAINTS AND A ROLE FOR SEXUAL SELECTION

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The number of offspring per litter is highly variable among mammalian species. In mammals, in general, it appears that small and medium sized species tend to produce many offspring per birth while large species tend to bear only one. However, there are big differences in litter size among species of similar size. Moreover, there is not a continuous relationship between Litter Size and Body Weight. If we look at the Figure 1, we will see that above certain threshold of body mass, litter size is 1; and below the threshold there is a great variability. But why should there be a threshold?

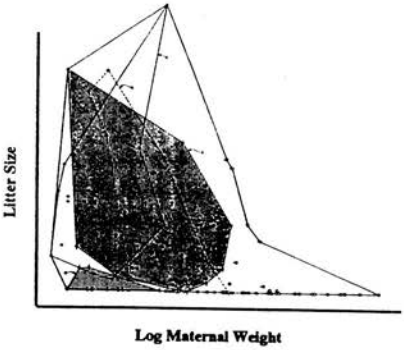

Figure 1.- Mean litter size plotted against body size for the class Mammalia. Convex polygons outline major ordinal groupings (Modified after Eisenberg 1981).

Metabolic rate scales at 0.75 power with body mass. The "mass specific" or "relative" metabolic rate, which is the metabolic rate divided by body weight, scales at -0.25 power with body mass (Hemmingsen 1960). The slope of many specific relationships, such as mass flow, biomass production or parental effort, relative to body weight are around this figure (Peters 1983; Reiss 1989). Metabolic rate appears to set an upper limit in the relative amount of energy that a mother can allocate into offspring - i.e. larger mammals invest relatively less. The percentage that litter weight represents with respect to mother weight decreases with mother weight to the -0.25 power. Robbins & Robbins (1979) show this relationship for ungulates and subungulates.

Relative weight of individual newborn does not decrease in the same way. For eutherian mammals, and despite some variability, it appears to be roughly around 5% of maternal body weight (Land 1985). One consequence emerges. We should expect very large mammals to have to cope with the problem that maximum possible litter weight could be smaller than optimal individual newborn weight. This would set an upper limit on mammalian size range (Land 1985). But another consequence could also be recognized. On going down from such a maximum maternal size, twinning is not possible until maximum litter weight can be two-fold the individual newborn weight

(Fig.2). This sets an upper limit on size for mammals having multiple births. Such a limit is roughly around 400 Kg maternal weight (see Robbins & Robbins 1979). No mammal species regularly bears twins above such a threshold. Therefore, our goal at this point should be to explain the variation in litter size for mammals below 400 Kg., which in turn comprises the whole extant variation.

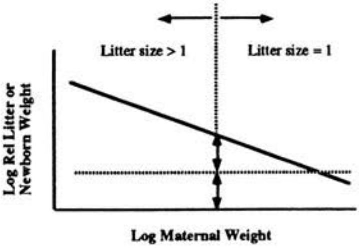

Figure 2. - Hypothetical relationship among litter and newborn weight with maternal weight, which would explain the threshold for litter size reduction to one.

Latitude also appears to affect litter size. May & Rubenstein (1985) made a regression of average litter size to body weight for a compilation of mammalian species. They assigned every species to one of three geographical zones, namely tropical, temperate or arctic. Three regression lines for geographical areas showed the general pattern of decreasing litter size with increasing body weight, together with a tendency towards larger litters upwards along the tropical-temperate-arctic gradient. The range from K to r selection as we go up to the poles is one possible explanation (May & Rubenstein 1985), although seasonality in reproduction is also likely to have an effect (Eisenberg 1988). Anyway, this result reccomends to take into account the latitude effects, when seeking for any other influences on litter size.

At this point we need a new hypothesis to explain the remaining variation within areas, and this is why I would like to present here my hipothesis of sexual selection and litter size. Sexual selection is a kind of selection which usually affects body mass. Male-male competition for mates normally involves the development of weapons together with an increase in male body mass with respect to that of the female (Clutton-Brock 1982; Jarman 1983; Hedrick & Temeles 1989). Polygynous mating systems are typical of mammals (Clutton-Brock 1989) and they are closely related to the development of size dimorphism (Ralls 1977; Lande 1980).

Sexual selection acting on male body mass can affect the shape of the curve which relates the success of an offspring to the amount of care it receives. By means of increasing the variance in reproductive success, it can change the shape of the curve and reduce the expected fitness of the offspring when it receives a lower amount of investment. Thus making more profitable the production of one good offspring instead of two medium sized offspring (Fig. 3). Although this kind of selection would act primarily on *male* body mass, the same basic relationship can also be applied to female offspring since birth weight in females influences birth weight of their offspring of both sexes (Clutton-Brock et al. 1988). Therefore, even though the strength of selection is likely to be different, selection for male body mass should also affect investment in female newborn body mass, due to the costs otherwise involved for the next generation. Our beginning hypothesis should be, therefore, that sexual selection for male body mass favours female reproductive strategies of single birth parental allocation.

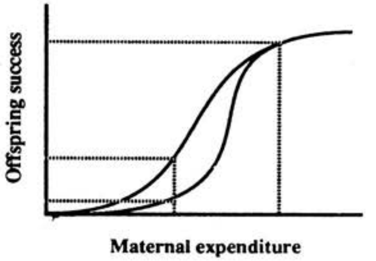

Figure 3.- Hypothetical relationship between offspring success and maternal expenditure. When sexual selection for body mass affects the shape of the curve, the partitioning of expenditure into several offspring become less profitable.

The proper hypothesis to be tested would be that the higher the variance in male reproductive success due to maternal investment, the lower the frequency of multiple births. Unfortunately, such information is not available for most mammalian species. Since it is assumed that a high variance in males' reproductive success due to body size would probably lead to a sexual weight dimorphism (Hedrick & Temeles 1989), we can consider a less direct but more testable hypothesis, which would be that the higher the sexual weight dimorphism, the lower the mean litter size.

In order to remove the variance due to constraints from body weight and latitude, I focused the analysis on temperate-arctic species and female weight up to 400 Kg. I followed the comparative method described in Pagel & Harvey (1989) and Harvey & Pagel (1991). It is based on the comparison of species or higher nodes that share a common ancestor in a phylogenetic tree. Pairwise comparisons can be considered independent evolutionary events, and then be used to test the relationship between variables.

Independent contrasts for all mammalian species considered, revealed a negative relationship between Litter Size (LS) and Weight Dimorphism (WD; r=-0.508; N=66; p=0.0001; Fig. 4a), which remained after removing the effect of Female Weight (FW; $r_{LS\ WD.FW}$=-0.476; N=66; p=0.0001; Fig. 4b).

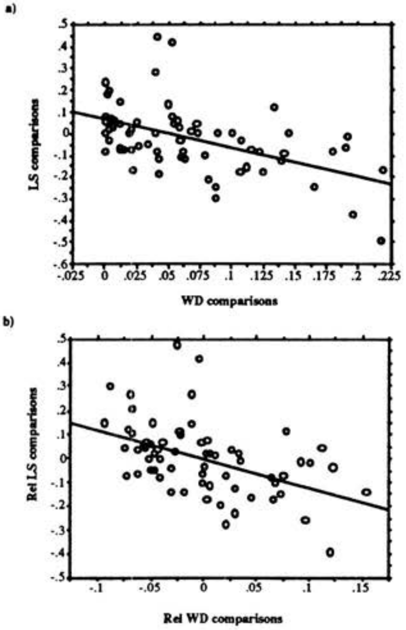

Figure 4.- Independent comparisons of Litter Size (LS) at nodes in the phylogenetic tree plotted against independent contrast of weight dimorphism (WD) for temperate -arctic mammals. Rel means relative comparisons after removing the effect of Female Weight (FW). All variables were log-transformed before computing the differences.

In order to see whether the relationship remained at two different levels of the phylogeny, I separated the independent contrasts into two groups according to their height in the phylogenetic tree. One group was constituted by all those comparisons below the family level (comparisons at low

Table 1.- Correlations of WD and LS, after removing the effect of FW, for independent contrasts in nodes at two levels of the phylogenetic tree (high: family level and above; low: below family level), for three taxonomic groups (L+R+I: Lagomorpha+Rodentia+Insectivora; C+P: Carnivora+Pinnipedia; U+C: Ungulata+Cetacea), and for three body-weight groups for FW. r= correlation coeficient; ß=slope of the relationship; N=number of independent comparisons. ***=p<0.001; **=p<0.01; *=p<0.05; ns= non significant.

	PHYLOGENETIC LEVEL		TAXONOMIC GROUPS			BODY-WEIGHT GROUPS		
	HIGH	LOW	L+R+I	C+P	U+C	<1kg	<10kg	>10Kg
r	0.550**	0.445**	0.488*	0.491*	0.385ns	0.824***	0.486**	0.428*
ß	-2.071	-0.788	-1.878	-1.310	-1.011	-2.461	-1.362	-1.076
N	29	37	23	18	24	13	33	32

level in the tree) and the other by the remaining, including family level and above (comparisons at high level in the tree). The relationship was held at both levels, even after removing the effect of FW, although it appeared to be stronger at a higher level in the tree than at a lower level (Table 1). The same relationship was tested within different taxonomic groups (Table 1). In all of them there appeared to be a negative relationship between WD and LS, although this did not reach significance for Ungulates. Both significant relationships remained after removing the effect of FW. On the other hand, the relationship between FW and LS for these groups was only significant for Carnivora, and what is remarkable is that the slope of the relationship was positive in the case of the first group (Lago+Rode+Insect), and negative for the other two, while for WD the relationship with LS was negative in all cases. In order to gain further insight on the effect of female weight, I made regressions of WD on LS for different body-size groups. In all cases there appeared to be a negative relationship between LS and WD (Table 1). With FW, on the contrary, LS tended to increase in small mammals (with non-significant relationships), and decreased significantly in bigger mammals. Moreover, in bigger mammals the effect of FW in explaining LS was greater (r=0.542) than that of WD (r=0.501).

Sexual weight dimorphism has been so far considered just as the ratio of male to female body weight. We could hypothesize that two-fold size does not involve the same cost for a small than for a big animal, if we take into account the differences in metabolic turnover among sizes. Thus, a value of two in sexual dimorphism could be not comparable between large and small animals. Weight dimorphism -male weight divided by female weight- means, for our purpose, something related to the optimal body weight to be produced divided by the amount of resources available to cope with it. But in fact, the budget a female owns to devote into offspring weight is not related to her body weight but to her metabolic weight. One could predict that a given strengh of sexual selection acting on body weight would lead to a higher degree of dimorphism the smaller the species is. This prediction is based on the assumption that increasing in size is more constrained the

Table 2.- Correlations of Metabolic weight dimorphism (Met.WD) with litter size (LS) for different groups of temperate mammals. r = correlation coefficient; β = slope of the regression line; n = number of independent contrasts; * = p<0.05; ** = p<0.01; *** p<0.001; ns = non signifficant.

	Met.WD with LS			Met.WD with LS (After removing the effect of FW)		
	r	β	n	$r_{MetWD\ LS.FW}$	β	n
TEMPERATE MAMMALS	0.379**	-0.331	66	0.342**	-0.616	66
LAGOMORPHA+ RODENTIA+ INSECTIVORA	0.135ns	0.099	23	0.180ns	-0.230	23
CARNIVORA+P	0.540*	-0.424	18	0.194ns	-0.481	18
UNGULATA+C	0.498*	-0.596	24	0.388ns	-1.027	24
BELOW 1KG FW	0.312ns	0.221	13	0.018ns	0.018	13
BELOW 10KG FW	0.078ns	0.062	33	0.151ns	-0.209	33
ABOVE 10KG FW	0.634***	-0.658	32	0.432*	-1.097	32

bigger the animal is. I worked out a measure of sexual weight dimorphism by dividing male weight by female metabolic weight (which is: female weight to the 0.75 power). I called this new measure Metabolic Weight Dimorphism (Met.WD), and tested its relationships with Litter Size (Table 2). LS decreased with Met.WD for temperate mammals in general, although the groups responsible for such a trend were those of larger size, i.e. Carnivora, Ungulata and especially all those taxa above 10 Kg FW (Table 2). The relationship appeared to be stronger than for classical WD in both Ungulates and all taxa above 10 Kg FW. The constraint by metabolic size appeared, therefore, to be useful to explain LS in bigger animals.

The results presented here support the hypothesis that increases in weight dimorphism are accompanied by decreases in litter size. Variation in weight dimorphism can explain an important proportion of variation in litter size among mammals. This is especially remarkable since litter size has been traditionally considered to be affected by number of different factors, either physiological and ecological ones (i.e., body weight, latitude, diet, basal metabolic rate, etc.; Eisenberg 1981; May & Rubenstein 1985; Boyce 1988). Those multiple factors influencing litter size can be responsible for the relatively lower predictability of litter size from weight dimorphism at a low level in the phylogenetic tree. The macroevolutionary pattern is more evident, probably because at this level the averaged values at higher nodes promediate an important amount of the variation due to ecological factors.

An important source of confidence on

the relationship between weight dimorphism and litter size comes from the fact that the negative trend remains in every taxonomic group. The results show an amount of residual variance for smaller changes in weight dimorphism - i.e. when the force towards litter size reduction is slight. However, this should be expected considering that a number of other factors can influence litter size, and what is important in favour of the hypothesis of sexual selection is that when it is present with a noticeable strength (high weight dimorphism), in most cases it is able to produce a reduction in litter size in spite of other forces.

To summarize, several new constraints have to be considered to explain litter size in mammals:

1) The threshold of body weight which makes impossible twinning in very large mammals (due to constraints by metabolic rate)

2) The sexual selection for male body mass as a force against multiple births, and

3) When sexual dimorphism is used as a measure of sexual selection for male body mass, it has to be corrected by metabolic weight to better explain the reduction of litter size in bigger animals.

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Proximate and ultimate determination of avian reproductive decisions

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Both laying date and clutch size have important consequences for the number of surviving offspring. In the past 40 years since David Lack's seminal papers on avian reproduction (Lack 1954), a great amount of work has been devoted to the evolutionary basis of these decisions (Martin1987). However, our understanding of the physiological basis of reproductive decision-making lags far behind. I will review some models and studies dealing with reproductive decisions from the proximate point of view.

A set of models on the relationship between energy reserves and breeding schedule began with Darwin (1871) and was given the most explicit treatment by Price et al. (1988). In them energy reserves place a direct linear limitation on breeding schedule: the larger the storage reserve or food availability prior to breeding, the earlier that breeding is initiated. As an alternative to the 'linear model', Schultz (1981) has proposed the 'saturation point model'. Below a certain level of reserves, breeding is delayed as the linear model predicts. Above the saturation point limit, however, breeding date is unrelated to level of reserves. The evidence from experimental food supplementations suggests that the relationship between breeding time and energy reserves often contains a saturation point (Schultz 1981). Saturation points can be due to the reproductive system of all individuals being triggered at the same time by the same factor (photoperiod, rainfall, etc.), which is independent of the nutritional status of the individuals. The best proximate factor would be that which predicts food availability for the time when chicks have to be fed. The two proximate determination mechanisms, i.e. directly by food supply (linear model) or by an environmental cue (saturation point model), have different implications with respect to the ability to exploit unpredictable resources (better with food supply determination) and the risks of not predicting future food supply (higher for direct food supply determination). The point is, that only for directly food limited breeding schedules, is there a need to explain why in spite of early breeders being the most productive, there is no directional selection for earlier breeding dates in avian populations (Perrins 1970, Price et al. 1988). If saturation points occur, laying date is constrained by the common time threshold and no selection is expected. Only a change in the time threshold is expected if the environment induces changes in the optimal laying date.

Under both proximate models, changes in food supply at laying may deviate from a general trend. Such deviations may be unrelated to future food supply. Under these conditions, females would lay erroneous clutch sizes with respect to their parental quality. Parental quality is the capacity to raise healthy young, and is positively associated but not equivalent to clutch size if errors do occur. If we assume that each parental quality has an optimal clutch size, that the proportion of positive and negative errors with respect to the optimum is the same for each parental quality category, and that extreme parental qualities are less frequent than intermediate qualities, then we would expect that erroneously enlarged clutches are more frequent among the largest clutches, while erroneously reduced clutches will be more frequent among the smallest clutches. Thus, fitness in relation to clutch size may be greater for intermediate than for large clutches, while the relationship between fitness and parental quality remains linear. Also, in bad years, the large clutches containing a greater proportion of positive errors will be more adversely affected, increasing the interyear variance for the greatest clutch sizes, as observed in some studies (Boyce & Perrins 1987). The idea of individuals making errors in predicting future conditions (Aparicio, MS) reconciles the evidence for individual optimization of clutch size (Drent & Daan 1980, Gustafsson & Sutherland 1988, Pettifor et al. 1988) with the observation of declining parental feeding rates, starvation of young and reduced survival probabilities in the largest broods (Klomp 1970, Magrath 1991). No assumptions about heritability of life history characters are needed, only that quality as such and the probability of making errors are not heritable, which seems reasonable given the potential of age, individual experience and environmental effects during development as determinants of these characters.

Based on their detailed field and laboratory studies of European kestrels, Daan et al. (1988) have proposed an elegant model explaining how laying date determines clutch size in temperate environments. Given that the reproductive value of eggs declines with laying date as shown for several species, the optimal clutch size should decrease with laying date independently of the seasonal trend in food availability. Even if food availability increases throughout the season, as is the case in some species, the trade-off between waiting for food availability to allow for more young to be fed and the decrease in the reproductive value of these young favours decreasing clutches with season. The model postulates the existence of a condition threshold decreasing with time, which is governed via an internal annual program or via some external variable. However, there are several pieces of evidence which indicate that the fixed laying date-clutch size relationship model is not generally applicable. In a food supplementation experiment with Spanish kestrels, J. Aparicio (Aparicio, in prep.) has found that: 1) although there was a decreasing trend of clutch size with laying date in the population, the largest clutches were not always the earliest; 2) clutches were significantly larger for the supplemented than for the non-supplemented pairs, although there was no significant difference with respect to laying date; 3) clutch size did not decline with laying date in the supplemented group, and 4) the minimum laying date in the population was not advanced by supplementation. The first three results contradict the hypothesis of a fixed laying date-clutch size relationship, while the fourth supports the saturation point model. The independence of laying date and clutch size, contrary to the fixed condition threshold model, has been observed in other experimental studies (Hochachka 1990, Hörnfeldt & Eklund 1990, Nilsson 1991). A general model of clutch size determination has to envisage situations in which such a fixed threshold would not be adaptive.

The fixed condition threshold model is mechanistically linked to a seasonal rise in prolactin levels in females during the breeding season (Meijer et al. 1988). This increase is accelerated as soon as laying begins, inducing a rapid rise in incubation time. When prolactin levels reach a certain threshold, resorbtion of remaining follicles in the ovary and thus cessation of laying occurs. As the acceleration of prolactin levels is induced from increasingly higher levels as the season progresses, the prolactin threshold will be reached after a decreasing number of eggs has been laid, leading to the seasonal decrease in clutch size. However, the seasonal rise in prolactin levels could also be induced by the increasing need to start incubation early in the laying process to reduce the loss of viability of the first-laid eggs. The rate of viability loss of unincubated eggs would increase during the season due to higher ambient temperatures, which would sooner induce uncontrolled embryo development (Veiga 1992).

The rising prolactin model incorporates fixed laying intervals between eggs. However, these intervals do vary depending on food availability. In the kestrel experiment referred to earlier (Aparicio in prep.), supplemented females had shorter laying intervals than control females. Clutch size was negatively related to laying intervals and positively to the time taken to lay the whole clutch. Laying date had no independent effect on clutch size, when laying intervals were controlled for. Prolonged laying intervals, implying energy stress on the laying female, could induce the hormonal changes necessary to produce cessation of laying.

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PARENT-OFFSPRING SYMBIOSIS: RESOURCE EXCHANGE AS PRECURSOR TO AFFECTIVE EXCHANGE AND THE EVOLUTION OF SOCIAL BONDS

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The phylogenetic breadth and depth of social bonds present a challenging evolutionary puzzle. While the *functions* of social bonds seem apparent, their likely evolutionary origins and phylogenetic elaborations do not. Recent psychobiological investigations of parent-offspring relations in Norway rat offer new clues to proximate mechanisms of behavior and affective responses that may help decipher the evolution of social bonds.

Maternal behavior in Norway rat (*Rattus norvegicus*) consists of an organized cycle of stereotyped activities, *viz*., nursing and brooding, licking the young, nest-building, and carrying. It is common to describe and interpret in adaptive terms each of these activities and the overall maternal behavior cycle, emphasizing "parental investments" of time, resources, and skills that compensate for the offspring's infantile deficits and benefit the parent's lifetime fitness. This perspective usually highlights the unidirectional flow of resources from parent to offspring, and thus sets the stage for analyses of parental investment and of the prediction of "conflict" that arise when the economics of parental interests clash with those of the offspring.

Licking of the young is a common component in the parental repertoire of many species. In rat, this licking is directed at the infants' anogenital region and provides to the young stimulation that provokes voiding. Such maternal licking compensates for the pups' inabilities, improves nest hygiene, makes the nest less obvious to predators, enhances the young's bloodflow and arousal, and leads to other consequences that offer helpful support to them at a vulnerable time of early life.

But it has been discovered that there is more to such parental licking than providing vital stimulation to needy offspring. By injecting radioactively-labeled water into some of the pups in a litter and tracing the fate of the label one day later, it was found that mother rats not only lick the pups and stimulate urination, but the

the dam also ingests the urine. Quantitative, developmental studies of this urine ingestion revealed that the rat dams ingest (reclaim) about 2/3 of their lactational water transferred to the pups the day before. Additional experiments documented that this water resource is both physiologically and behaviorally significant to the dams.

Other studies have demonstrated that resources such as thermal energy, mechanical energy, immune competence, endocrine factors, and electrolytes fit into a similar framework of bi-directional exchange between parent and offspring. The metaphor of *parent-offspring symbiosis* provides a clear guide to the rule that mutually beneficial consequences can derive from interactions that are determined by individually and autonomously controlled behavior. That is, symbiotic exchanges are ruled by parent and offspring regulating themselves, not the exchanges.

Quantifying the value of physiological and behavioral resources is further complicated by the ability of each participant in a parent-offspring symbiosis to alter the perceptions of the other. For instance, suckling rat pups magnify the mother's salt appetite and enhance her perception of the meager salinity of their hypotonic urine. It can also be shown that stimulus contingencies within the family system can establish conditioned associations between previously neutral stimuli (e.g., an odor) and behavioral or physiological responses. Cues with such potency can also be part of the interindividual exchanges.

Experiential mechanisms that modify the value of physiological commodities, or induce perceptions that create new commodities for a symbiont, contribute to *affective* exchanges. This can be viewed as fundamental to the establishment of social bonds. A gradual, evolutionary process can be conceptualized: Parents and infants applied extant mechanisms for individual homeostasis in the regulation of their interactions. In the case of licking, for example, the dams' behavior is controlled by mechanisms that derive directly from those that govern body fluid and electrolyte balance. These mechanisms are susceptible to modulation by factors, such as hormone titers, that offspring can affect both directly and indirectly.

As part of this abbreviated overview, attention was given also to human language. It was posited that word usages reflect links between somatic and affective dimensions that are consistent with the symbiosis model. For example, words for *warm* and *cool* have both thermal and affective meanings. In the affective domain, warmth generally connotes closeness and a positive valence, whereas coolness connotes the opposite. Examination of extant languages with maximally remote ancestry (languages with Proto-Uralic versus Indo-European roots), revealed that this thermal-affective duality was consistently expressed and has apparently evolved independently in both linguistic lines.

This perspective on resource exchange and parent-offspring symbiosis thus helps focus attention on novel behavioral mechanisms in both parents and offspring. It does not reject the existence of conflict within the parent-offspring system, but recognizes mutualistic relations where they have been previously overlooked. We can better formulate hypothetical but plausible evolutionary pathways from resource exchange to exchanges of stimuli that have experience-based qualities, and place these interchanges within a framework of mechanisms underlying the regulatory systems used for maintenance of homeostasis.

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SOCIAL STRUCTURE

Environmental Conditions and Social Organization

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Ecological circumstances ultimately influence how animal societies develop. Typically, female reproductive success is limited by critical resources and as a result the abundance and distribution of these resources shape female relationships and associations. In turn, male relationships and associations primarily depend on those of females and it is this interaction among intra- and intersexual relationships that defines a species' social organization. In some instances environmental influences are so strong that different populations exhibit social variations that revolve around a common theme. Yet despite the crisp logic of, and broad qualitative support for, this hierarchical scheme, a detailed mechanistic understanding of how foraging, agonistic and affiliative decisions by individual females over resources, and by males over females, produces a social system is incomplete.

The purpose of this presentation is to begin highlighting the basic elements of such a framework. Understanding how simple behavioral responses to physical or social environmental factors can not only account for the array of social organizations exhibited by a group of related species such as grazing ungulates, but also how mechanistic responses can shape the species-specific patterns of natal dispersal that often lead to sex-specific biases in philopatry, the tendency of youngsters to remain near home when fully developed.

Primate Social Systems and the Social and Reproductive Decisions of Males: Constraints on and Consequences of Alternative Individual Strategies.

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Introduction

At any given time, organisms must make several "decisions" in order to cope successfully with the various problems of survival and reproduction that they have to resolve (for example, avoiding predators, feeding, mating, rearing and socializing) in the species-typical social and ecological niches where they happen to live in. Both inter-specific and intra-specific analyses have shown that, in fact, much of the variation observed in the "decisions" made appears to be of adaptive value (Lott 1991, Krebs and Davies 1991).

If we ask, for example, the general question: why individuals who live in complex social systems differ in the decisions they make ? then there are a number of conceptual problems that need to be clarified before we embark in answering the question. First, I am using the word "decision" to mean the particular course of action taken by an individual. I am making the assumption that, in theory, individuals have the possibility of making different decisions, not just one. Second, every decision can be considered one of the several possible determinants (or causes) of the decision(s) to be made later on and/or the consequence (or outcome) of the decision(s) made previously. Finally, we must make clear that (a) individuals may not show any significant variation in the decisions they make; (b) some decisions may have benefitial social and/or reproductive consequences for the individual who makes them but even so they may not correlate with any component of the individual's fitness; (c) some decisions may be adaptive (for example, some decisions may correlate with an individual's reproductive success) but they may still be of no evolutionary consequence (if variation in decisions does not correlate with variation in genotypes) (see Endler 1986).

The thesis of this paper is that by identifying and analysing the mechanisms which drive the individuals' decisions during their lifetimes we can get a better understanding of the adaptive value and evolutionary implications, if any, of observed inter-individual variation in social and reproductive decisions. As it has been repeatedly pointed out by Robert Hinde (e.g., 1970, 1982), the degree of generalization of a theory is inversely related to the extent with which it can accurately predict specific courses of action, outcomes, or "decisions". When someone, like myself, is especially interested in predicting and understanding the specific factors that drive an individual's decisions (Colmenares 1991, 1992) then it turns out that the integration of "how" and "why" questions provide the best pay-offs. The functional approach may suggest long-term end goal-states which should inform individuals about the appropriate direction in the decisions they make at every stage of their ontogenetic trajectories, given certain internal and external constraints. The study of mechanisms may tell us what are the immediate constraints (perturbations) which cause directional persistence or changes in the individuals' decisions during ontogeny and whether such changes are (i) essentially random, (ii) driven by short-term (proximate) causes and (intermediate) ontogenetic goals or (iii) they are driven by long-term (ultimate) causes and (end) ontogenetic goals.

Social and Reproductive Decisions of Male Baboons

Hamadryas baboons (Papio hamadryas) are Old World monkeys who live in complex social systems comprising several nested groupings (bands, clans and harems). Unlike most other primate species, and even mammals (Dunbar 1988), the dispersing sex in hamadryas baboons is the female (Kummer 1984). This paper presents data collected in the large colony of hamadryas baboons housed in an open enclosure at the Madrid Zoo. The colony has been shown to display the social organization typical of this species in the wild (Colmenares 1992). The data presented here were collected from June 1972 through August 1992. There are two data sets which were recorded in different periods: 1972-1985 (colony I: size ranged from 26 to 91 individuals, including 18 adult males) and 1985-1992 (colony II: size ranged from 40 to 78 individuals, including 15 adult males).

Were the tactical decisions made by males at a certain point in time predictive of tactical decisions made later on in their ontogenetic trajectories? Did particular tactical or strategic decisions have higher pay-offs ?

I analysed the following "tactical decision": (1) age at which the first adult female was acquired (colonies I and II), and the following "strategic decisions" (sequence of tactical decisions during ontogenetic trajectory): (2) mean number of oestrous females monopolised (colony I), (3) mean percentage of adult females monopolised (colony II). The fitness-related outcomes studied were: (4) age at which the first offspring was produced (colonies I and II) and (5) breeding rate per year (colony I). In all these measures, males showed large variation.

As it is shown in Table 1, the answers to these two questions were negative: there was no significant correlation between the various tactical and strategic decisions studied. Also, no tactical or strategic decision correlated with the fitness-related measures studied. In other words, if a male made the decision of starting to acquire females early in his reproductive lifespan, this would not necessarily mean that he would have offspring earlier than others who had started their reproductive careers later or that he would have higher reproductive success than the latter.

Short-term or long-term consequences of particular tactical decisions ? Were strategic decisions consistent ?

In order to answer to these questions, I analysed tactical decision (1) and the strategic decision (3) (see above) by examining the percent of females that each male owned at five 6-mo. age points (between ages 7.0 through 9.0). I also studied the fitness-related measure (4). In theses analyses I only used data from colony II.

Table 2 shows that (i) the first tactical decision made in the male's reproductive career, that is, when to acquire the first adult female did not predict how successful they were going to be later on, specifically between ages 7.0 through 9.0; (ii) the males who had their first offspring early in their reproductive careers tended to monopolise a greater number of female resources at ages 7.0 and 7.6; and (iii) most tactical decisions had short-terms effects, that is, they were only predictive of the trajectories followed by the males within the next six or twelve months, at most.

Were the tactical decisions made by males at different times of their reproductive careers influenced by some demographic factor ?

Table 3 shows that, especially the ratios of adult males to adult females and of older adult males to adult females appeared to be the main determinants of the tactical decisions made by the males, as measured by the actual percent of adult females that they monopolised at six different age points of their reproductive careers.

Conclusion

The results of the preliminary analyses presented here demonstrated (1) the existence of large variation both in the tactical and in the strategic decisions made by adult male baboons of two different colonies (n= 34 males); (2) the existence of large inter-male variation in at least two fitness-related measures: age at which first offspring was produced and breeding rate per year; (3) the lack of any relation between variation in tactical and strategic decisions and variation in the fitness of the incumbent males; and, finally, (4) that the tactical decisions made by the males at each age point, and the sequence of tactical decisions (strategic decision) made over their reproductive lifetimes, were better predicted by current demographic conditions (external constraints) than by the previous decisions that they had already made.

These results have some important implications in relation with the major topic addressed by this workshop. They suggest that direction in a male's social and reproductive ontogenetic trajectory may be determined mainly by current social constraints (that is, the decisions of the other individuals in the group) rather than (1) by past social achievements or (2) by long-term adaptive goals (that is, maximising fitness). In other words, in some higher animals, direction and rate in behavioural ontogeny may be best predicted by analysing the short-term effects of the interaction between the phenotypes and the constraints imposed by current environments than by assuming long-term goal-directedness. Individuals behave like stochastic, short-term goal-directed systems. The states (for example, defined by direction) of the system during ontogeny are not random but they may be highly variable. Prediction of concrete directions will need much more research and conceptual advance in the integration of our knowledge on mechanisms and functions. Knowledge of the end goal-state of a given system may help to hypothesize about the direction(s) it is most likely to follow during its lifetime, *given certain environmental circumstances* and *given certain more or less variable modes of reacting to circumstances* (that is, how the circumstances constrain the system) (see Dunbar 1984, for an excellent illustration of the productivity of this approach). However, the study of mechanisms is the only tool we have to assess the role of circumstances and constraints in driving the changes in the direction of systems (in our case, social and reproductive decisions of individuals) in ontogeny and in evolution, especially if (a) the degree of variation in direction is very large and (b) if the principle of equifinality is at work (e.g. Caro and Bateson 1986).

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Table 1: Correlations between different tactical and strategic decisions and reproductive outcomes*

Tactic Strategy Outcome	1	2	3	4	5
2	+0.38(I)	X	X	X	X
3	+0.08(II)	X	X	X	X
4	-0.23(I) +0.61(II)	-0.35(I)	-0.31(II)	X	X
5	+0.52(I)	X	X	-0.51(I)	X

* Tactic: age when first adult female acquired (1). Strategies: Mean number of oestrous females monopolized (2) and mean percentage of adult females monopolized (3). Outcomes: age when first offspring produced (4) and breeding rate per year (5). Body of table are Spearman Rank Correlation Coefficients. I and II in parentheses denote colonies I and II, respectively. None of the correlations were statistically significant. N's ranged from 8 to 11.

Table 2: Correlations between tactical decisions (age when first adult female acquired and mean percentage of adult females monopolised) made at different age points in ontogeny (from 7.0 until 9.0) and an intermediate outcome (age when first offspring produced)*

Tactical Decision/Age	7.0	7.6	8.0	8.6	9.0
Outcome/Age					
1	NO	NO	NO	NO	NO
2	YES	YES	NO	NO	NO
3	XX	YES	NO	NO	NO
4		XX	YES	YES	NO
5			XX	YES	NO
6				XX	YES
7					XX

* 1: age when first adult female acquired (tactic). 2: age when first offspring produced (outcome). 3 to 7: mean percentage of adult females monopolized at ages 7.0, 7.6, 8.0, 8.6 and 9.0 (tactics).

Table 3: Correlation between demographic factors and tactical decisions made by males at different age points in their reproductive lifetimes*.

Mean Percentage of Females Monopolized at ages	7.0	7.6	8.0	8.6	9.0
Ratio: adult males/ adult females	0.008	0.01	0.06	0.17	0.22
Ratio: older adult males/ adult females	0.02	0.01	0.09	0.02	0.02
Ratio: same age adult males/ adult females	0.06	0.19	0.63	0.69	0.24
Ratio: younger adult males/ adult females	0.87	0.04	0.34	0.61	0.10

*Body of table gives p-values for the Spearman Rank Correlation Coefficients computed between the four demographic variables on Y-axis and the tactical decisions made by males at five age points.

Environmental and Cognitive Constraints on Group Size in Primates

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Animals live in groups in order to solve critical problems of survival or reproduction that adversely affect their fitness (i.e. their ability to leave descendents) As far as primates are concerned, the concensus is that the functional problem that favours group-living is either predation risk or defence of food resources (see van Schaik 1983, Dunbar 1988). Since living in groups incurs costs (such as competition for access to resources, increased day journey length, etc), the optimal group size for a given individual animal will be involve a trade-off between the advantages of larger group size and its costs.

Although natural selection can be expected to ensure the evolution of those mechanisms that are required to support a given functional outcome, it is becoming increasingly clear that we have to make a clear distinction between the world as seen by the individual animal and the world as seen by the evolutionary processes. This is especially true of species which have evolved the kind of phenotypic flexibility that allows individual animals to adjust their behaviour to the particular exigencies of the moment, as is likely to be the case with primates. The past decade of field work has shown us that we have hitherto greatly underestimated the behavioural flexibility of the higher primates in particular.

One consequence of this is that we need to distinguish very carefully between the different kinds of questions we ask about the behaviour of animals. When we are interested in general evolutionary problems, we do not need to worry so much about the proximate mechanisms. But if we are interested in the behavioural choices that individual animals make, then constraints imposed by become more intrusive. I shall illustrate this with two examples of how features of the system may constrain group size in primates: one concerns the fact that time is a limiting resource, the other concerns the constraints imposed by the cognitive capacity of the animal's brain.

Animals living in the real world face two important demands on their time. One is the need to acquire the nutrients they need both to survive and to create offspring (i.e. reproduce). In an attempt to understand how conflicting demands on animals' time budgets limit their decisions about group size, I developed a systems model of baboon (*Papio* spp.) socio-ecology (see Dunbar 1992a). This model used 31 populations of baboons for which quantitative data were available on group size, day journey length, time budget and climatic variables to derive multivariate functional equations linking these variables. This model has very high predictive power, being able to predict day journey lengths and time budget structure of an independent sub-sample of populations to within 0.44 standard deviations on variables that vary by as much as an order of magnitude across the sample populations.

Primate groups are unusual in two respects: one is the extent to which they are based on intense social relationships, the second being the way sophisticated cognitive abilities are used to exploit social knowledge about other individuals in order to create alliances. In the higher primates at least, social grooming is the main mechanism used to service the social relationships that bind the group together. The amount of time devoted to social grooming turns out to be a linear function of group size (Dunbar 1991). We can use this relationship in the model to examine the limiting size for baboon groups by asking at what group size the animals would run out of "spare" time if they converted all their surplus resting time to feeding, travel and social time. This limiting group size is a complex function of habitat quality. But it predicts the observed geographical distribution of baboons extremely accurately (Dunbar 1992a).

Analysis of the structure of time budgets reveals that animals living in marginal habitats suggests that they are obliged to give priority to foraging and travel over social and resting time. One consequence of this is that groups that exceed the ecologically limiting group size devote less time to social interaction than they ought to in order to maintain the group's cohesion. We would expect such groups to be socially fragmented. And indeed they are: groups that were described as fragmenting regularly during travel or as subsequently undergoing fission were significantly more likely to exceed the predicted maximum tolerable for that habitat than groups that did not fragment (Dunbar 1992a).

The significance of social interaction in primate societies raises the possibility of the second constraint, namely the limit that cognitive capacity might impose on the number of relationships that an animal can keep track of through time. Since it is neocortex size that has been largely responsible for the increase in primate brain size (both in comparison with other taxa and for the differences between species within the Order Primates), I examined the relationship between relative neocortex size and mean group size in different primate genera (Dunbar 1992b). Using the ratio of neocortex volume to the volume of the rest of the brain as a means of standardising for the effects of body size differences, I found a linear relationship between relative neocortex size and the mean group size for primates as a whole (Fig. 1). The regression equation accounts for a surprisingly high 76% of the variance.

Further evidence suggests that the constraint lies not so much in trying to keep track of the changing pattern of all possible dyadic relationships within large groups but in the size of the close knit coalitions on which the stability of these groups depends. This meshes well with the so-called Machiavellian Intelligence theory of primate social evolution (see Byrne & Whiten 1988). It implies that the constraint lies in individual animals' abilities to remember and manipulate information about the behaviour of a small clique of social companions whom they need to use as allies against other group members.

These analyses have a number of implications. First, it suggests that whether we examine the behaviour of animals "top down" (i.e. as an evolutionary problem) or "bottom up" (i.e. as decisions made by individual animals operating in a specific environment) makes a difference as to whether or not features of the system are mutable or act as constraints. Second, it suggests that if primates need to evolve larger groups in order to occupy a new more predator risky habitat, they first need to be able to evolve a larger neocortex size. Third, there may be dietary constraints on the ease with which this can be done, either because of the nature of the diet (low quality diets may limit the amount of spare nutrient that can be devoted to developing large brained neonates) or the limited time that animals have available for feeding (essentially a "throughput" problem).

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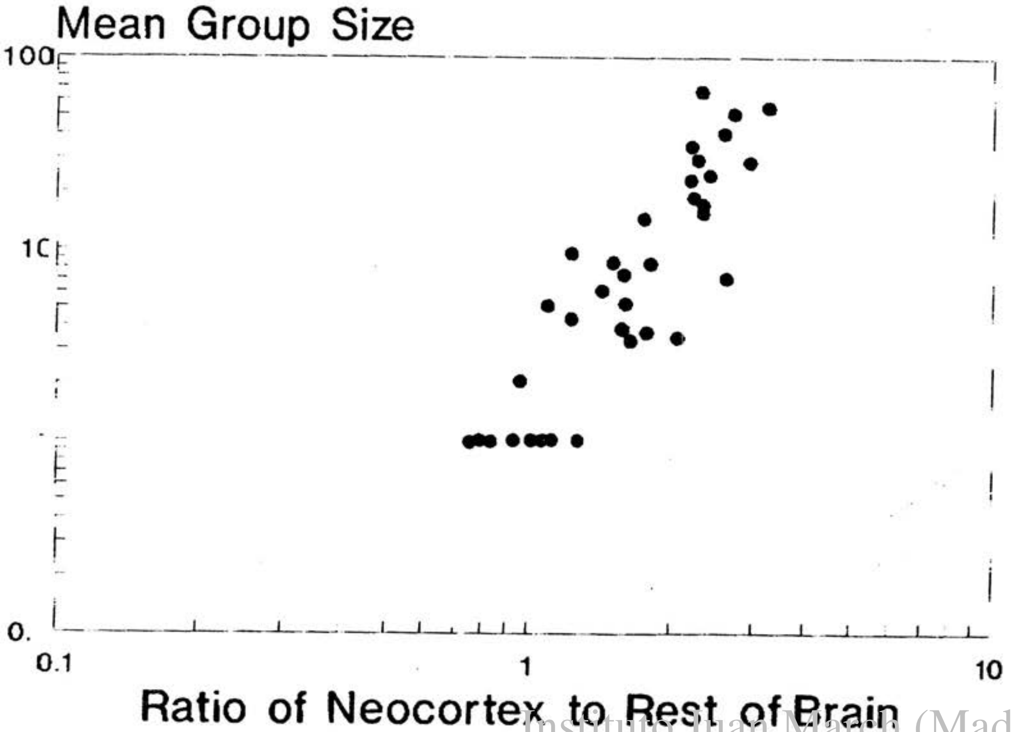
Legend to Figure

Mean group for individual primate genera, plotted against neocortex ratio (defined as the ratio of neocortex volume to the volume of the rest of the brain). Brain part volumes are based on data given by Stephan et al (1981). Data on group sizes for individual taxa derive from Smuts et al (1987). Redrawn from Dunbar (1992b).



MODES OF DEVELOPMENT

Parental care and offspring decisions about how to develop

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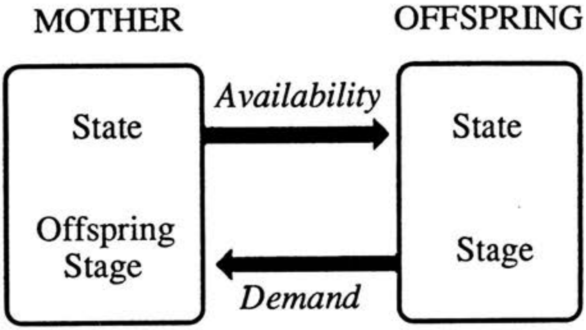
It has become obvious that members of the same species, the same sex and the same age may behave in dramatically different ways. "Alternative strategies" or "alternative tactics" within a species commonly arise because an individual has the capacity to respond in more than one way according to environmental conditions or its own body state (Caro & Bateson 1988). Such conditional responses during development are well known in the social insects, but they are also occur more frequently in mammals than had been realised. Young mammals may pick up crucial information from their mothers about when to wean themselves and how to develop afterwards on the basis of cues that they pick up from their nursing mothers. In an experiment on domestic cats, for instance, kittens of rationed mothers developed quite differently from those of mothers given *ad libitum* food, playing much more weeks after weaning as if they were preparing for an earlier break-up of the family group than the kittens growing up in a nutritionally rich environment (Bateson *et al* 1990).

In this experiment, the rationed mothers were less available to their kittens than mothers given *ad libitum* food, but their kittens put on weight as rapidly as the kittens of mothers given *ad libitum* food because they demanded more vigorously. Evidently, within certain limits, the mothers do respond to the behaviour of their offspring, but equally the kittens are responsive to their mother and change their developmental trajectory accordingly.

A mother may be sensitive to the condition of its offspring so that, if it is weak but reasonably well developed, she may forego a breeding opportunity in order to nurture it through to independence. Young have to be sensitive to the condition of their mothers and adjust their pattern of development accordingly since their mothers respond not only to the state of the young but also to their own condition. When food is in very short supply, mothers of many species wean much earlier than they would otherwise have done. The interplay may be summarised as follows:



The mother's nutritional state as well as the offspring's stage and demands influence the mother's availability. The offspring's state and stage of development together with the mother's availability influence the offspring's demands.

All this evidence from the study of mechanism forces a reappraisal of the optimal route to maximum reproductive success in mothers and the optimal route to highest probability of survival in their offspring. Genetic conflict of interest in parent-offspring relationships does not necessarily imply behavioural conflict. Indeed, contrary to popular belief, aggression between mother and offspring is rarely seen in mammals particularly at the time of weaning when it has been most avidly expected. The evidence suggests, however, a variety of other points that need to be fed into evolutionary arguments about what might be expected in the changing relationships between mothers and their offspring. First, young often have the capacity to adopt a phenotype appropriate to the environment into which they will have fend for themselves. They need to respond to information provided by the mother. Second, preparation for weaning in the young requires many changes in the gut and a constraint on how rapidly the metamorphosis of the intestinal anatomy and physiology can take place may require that offspring pay attention to cues from the mother. Finally, the young may also have to pay attention to the condition of the mother because of the need to take into account both the immediate effects of maternal care on survival but also the post-weaning contributions of the mother. The more they demand before weaning, the less they may get later because lactation is so costly to the mother. As consequence, mammals receiving post-weaning care are especially likely to wean themselves at an optimum moment. The evolutionary approach has to take into account the interplay between mother and offspring as they update information about each other.

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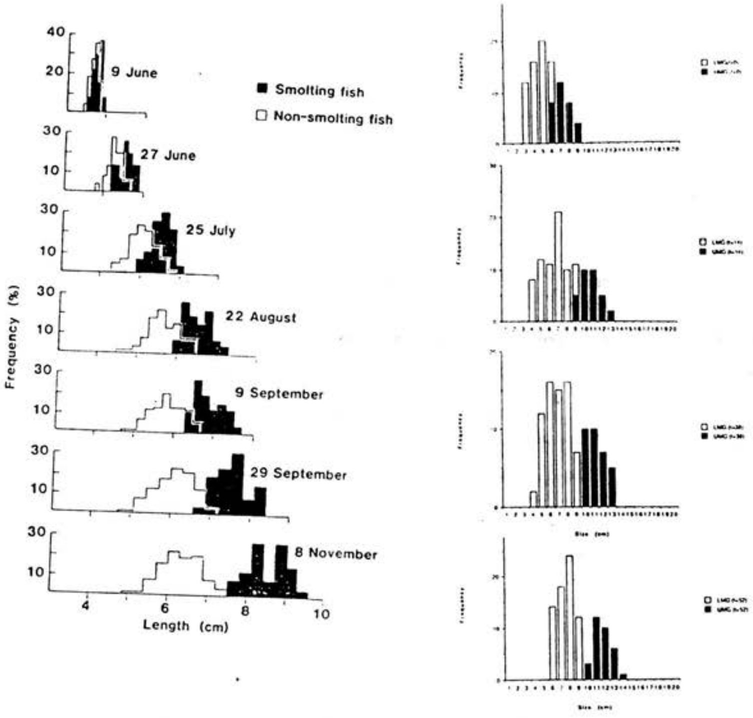
Developmental Switches and the Evolution of Life History Strategies Felicity A Huntingford, Department of Zoology, University of Glasgow, Glasgow G12 8QQ, UK.

Atlantic salmon (*Salmo salar*) have very variable life histories; for example, juveniles may spend between 1 and 7 years in freshwater before migrating to sea (smolting), where they may spend a futher 1-6 years before breeding. Recent work by FAH, with John Thorpe (Scottish Office Freshwater Fisheries Laboratory, Pitlochry, Perthshire) and Neil Metcalfe (Glasgow University Zoology Department), has shown that the distribution of lengths among siblings is initially unimodal but becomes bimodal by the autumn as some fish become anorexic (Thorpe *et al.* 1992; Figure 1a). Fish in the upper mode smolt the next spring, while those in the lower mode delay smolting. Initially, sizes of fish that eventually form the two modes overlap considerably. Evidence suggests that fish that grow well during a key time in July-August follow the early smolting route, while those that grow poorly at this time delay smolting. Similarly, only those adult fish that are relatively large and fat in January maintain gonadal growth and mature for the next breeding season.

Figure 1. a. Length frequency distributions for a population of real sibling Atlantic salmon in their first year of life. b. Simulated length frequency distributions generated by a dynamic programming model.

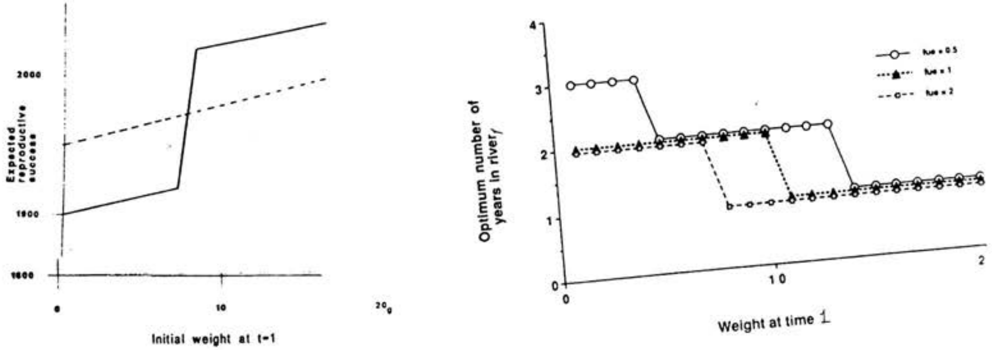


To elucidate the adaptive consequences of variable ages of smolting and breeding based on performance-dependent developmental switches, we have collaborated with Marc Mangel (University of California, Davis) in developing a model based on the method of stochastic dynamic programming. This technique extends classical optimality modelling by allowing the modeller to bridge the gap between events that may happen well before breeding and the ultimate fitness of the animals concerned (Mangel & Clark 1988).

The model currently refers only to females and assumes that the fish breed just once. A terminal fitness function relates a state variable (size) to fitness (fecundity). Change in size is modelled by equations defining anabolic and catabolic processes, with temperature-dependent seasonal trends and a seasonallyvariable food supply. An additional term (food utilisation efficiency) defines the efficiency with which each fish turns food in the environment into flesh. The parameters in the growth equation are derived separately for the freshwater and sea water stages based on our empirical data on fish housed in good growing conditions. For anorexic fish, the anabolic component is absent and the catabolic component is reduced to allow for the effects of feeding on metabolism. At the same time, predation risk is zero, since the model assumes that fish are only preyed upon while foraging.

Growth equations, size-predation and size-fecundity functions are used to calculate the lifetime reproductive success of fish of a given size at a given time depending on their subsequent life history decisions (in adults, to breed at the next opportunity or to delay; in juveniles, to smolt at the next opportunity or delay, in which case they may become anorexic). In this way we can identify the life history trajectory that maximises fitness for fish of a range of sizes at each time period. Thus, Figure 2a shows the reproductive success of juveniles of different sizes that spend 1 or 2 years in freshwater. Note that the lines cross, so small fish do best if they smolt at 2y, while large ones do best by smolting at 1y. This effect is driven by size-dependent predation during the smolt migration. Presenting similar data in a different way, Figure 2b shows the optimum number of years in fresh water for fish of a given weight and for different food utilisation efficiencies, which is higher for smaller fish and for those with low efficiency.

Figure 2a. Expected lifetime reproductive success for fish of different weights that remain in freshwater for 1 or 2 years. b. Optimal number of years at sea for fish of different weights and food utilisation efficiencies.



Running the model forwards generates growth patterns for fish of a given initial size following their optimal developmental routes (Figure 1b). The real data and the model's output fit well, in that populations of model fish become bimodal by late autumn, because smaller fish do best by delaying smolting and becoming anorexic. However, unlike real fish, model fish that form the two modes are already different in size in midsummer, because in generating these figures the model assumed a fixed food utilisation efficiency.

Although development of this model of life history variation is still at an early stage, it does reconstruct known phenomena such as variable age of smolting, condition dependent switches and the emergence of bimodal size distributions within cohorts, so the selective forces depicted in the model provide a *plausible* functional explanation for variable life histories. If it does turn out to be correct, we will have a powerful tool for exploring the selective processes acting on life history variants and the developmental mechanisms that control them. However, it is important to note that the model works because and only because it is based on an understanding of the mechanisms of growth in fishes. This information is needed to model changes in the state variable in relation to life history events. In the context of the present meeting, one of the great virtues of stochastic dynamic modelling is that it forces us to incorparate 'how' information into 'why' models and demonstrates what can be achieved when causal and functional approaches are integrated.

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MECHANISMS AND THE PATTERN OF EVOLUTION

SEXUAL IMPRINTING AND PLUMAGE EVOLUTION

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Theoretical models for the evolutionary process of sexual selection in birds are quite divers. Nevertheless they have one characteristic in common, which is that mate preferences and variations in preferences are always modeled as a consequence of the genetic constitution of the choosing individual. This assumption is crucial to the dynamics of the evolutionary process, but is it valid?

It is known for a long time that several bird species acquire their preference as a consequence of early experience with their parents, i.e. by the learning process of sexual imprinting. This process has, so far, hardly been considered as an important factor in sexual selection and I discuss three reasons as to why this may be so.

Objection 1: It has been stated that imprinting is limited to specific groups of rapidly evolving, sympatrical, groups of birds. This statement is based on several reviews published 20 years ago. An update of the existing evidence suggests that it is much wider spread than previously realized. Evidence for imprinting (including compelling case histories) is present for at least 13 of the 27 orders of birds, including the emu, penguins, birds of prey and owls. As imprinting seems to occur in any species where someone bothered to look for it, it may be the rule rather than the exception among birds (1).

Objection 2: Many textbooks mention that imprinting is often confined to one sex and that the other has an 'innate' or 'preprogrammed' preference for the appearance of its own species. Again, critical inspection of the evidence reveals that this is not true. For both mallard and zebra finch there is good evidence that cross-fostered individuals end up being paired with their own species as a result of being exposed to more (courtship)-

activity of the conspecific mate. When this factor is being controlled for, it turns out that cross-fostered and normal reared birds of both sexes choose mates resembling the rearing type. So, sex-differences in mate choice do exist, but they are either due to both sexes giving different weights to different aspects of their mates or (perhaps) to the sexes learning different things, but not because one sex learns the parental appearance and the other has an 'innate' preference for it (ref. 2,3). In species with uni-parental care, imprinting on siblings reaching maturity may provide a means of learning about the other sex.

Objection 3: Imprinting is usually assumed to lead to a preference for mates closely resembling the original stimulus, which would not provide a mechanism for evolutionary change. Recent research has indicated that there are at least two ways in which imprinting may lead to a preference for specific, differently looking mates. Japanese quail prefer mates which are slightly different from the ones they were reared with. When chicks are exposed to a white adult with blacks dots, they later on prefer a mate with more dots than the familiar stimulus rather than one with fewer dots (4). This gives a directionality to the preference for novel mates which may drive plumage changes (5,6).

The second mechanism which may produce evolutionary changes in appearance is suggested by experiments on zebra finches. Males raised by pairs consisting of two colour morphs prefer mates of their mother's phenotype later on. Nevertheless the father seems to contribute to the preference. However, the evidence suggests that males later on prefer mates dissimilar to the father. This suggests that discrimination learning is occurring with each parent having a different, more or less opposite effect on the later preference. Discrimination learning may give rise to a phenomenon known as 'peak shift' in which stimuli of a more extreme type than the training stimuli give rise to stronger responses than the original stimuli. Some preliminary data suggest the same to be true for imprinting. This effect may also give rise to preferences for specific, deviating mates and hence lead to plumage changes. The mechanism is also very effective in maintaining sexual dimorphism once occurred.

The wide spread occurrence of sexual imprinting, the absence of good evidence for sex differences in 'imprintability' and the mechanisms available for producing preferences for specific types of novel mates strengthen the importance of imprinting as a factor involved in the evolution of conspicuous features by means of sexual selection. Imprinting may alter the dynamics of the evolutionary process as birds with a parent which has a heritable novel trait will not only inherit the trait, but, by learning their parents appearance, will also take this into account in their later mate preference.

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Fluctuating asymmetry and the evolution of signals

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Signals are in some way or another produced by morphological characters. Most morphological traits (including those involved in signalling) demonstrate fluctuating asymmetry (FA) which occurs as usually small, random deviations from perfect symmetry. The degree of FA is primarily determined by the functional importance of a character, and therefore the prevailing mode of selection (Møller and Pomiankowski 1993). Characters subject to intense directional selection demonstrate elevated levels of asymmetry, while traits subject to intense stabilising selection have small degrees of asymmetry. FA reflects the ability of an individual to cope with a variety of environmental and genetic stresses, and asymmetry can therefore be viewed as a health certificate for the individual during development. Performance generally decreases with increasing asymmetry. One of the major advantages of FA as a means of assessment of performance is that we know the optimal solution which is symmetry. Studies of the functions and mechanisms of signalling have not fully exploited these facts.

Fluctuating asymmetry can be used to study the mechanisms of signalling at a number of different levels. First, FA is a snapshot of the interactions between an individual, its genotype and the environment during development of morphology. Since performance generally decreases with increasing asymmetry, FA becomes a mechanism and a test for how a genotype performs in terms of development of morphology. The morphology is the phenotype which is subsequently subjected to natural and sexual selection, and deviations from the optimum morphology result in selection against such phenotypes.

Second, FA represents a snapshot of how developmental homeostasis is maintained during ontogeny of a character. In other words, it represents a record of the developmental process if growth increments can be determined. The mechanism for development of asymmetry can therefore be unravelled.

Third, FA can be used in assessment of the quality of conspecifics (Møller and Pomiankowski 1993). The reason for this is that large degrees of asymmetry are costly in terms of performance. Preferences for individuals that perform well may thus also be preferences for individuals with little asymmetry. Signals are often under strong directional selection which reduces the level of developmental control and thus increases the level of FA. Small degrees of asymmetry in the exaggerated morphological basis for a signal reliably indicate an ability to cope with genetic and environmental stress. Many signalling characters demonstrate negative relationships between the size of a character and its degree of asymmetry. This demonstrates that individuals despite of developing the most extravagant signals still are able to produce these with little asymmetry. In other words, these signals provide reliable information on the ability to produce a perfect morphological basis for a signal. The selective part in the signalling system has several times been demonstrated to prefer symmetric signals over asymmetric ones (e. g., Møller 1992). This provided a mechanism for how reliability of signalling systems can be maintained, and how selection simultaneously acts for signal exaggeration and signal symmetry.

Fourth, most living organisms and their structural parts are bilaterally or radially symmetric, and individual organisms may have evolved sensory biases in their ability to discriminate between asymmetric and symmetric objects. Sensory abilities of organisms may have been biased towards detection of symmetry because food items, predators and competitors are symmetric. Symmetry therefore provides a potential mechanism for how perception of signal asymmetry has evolved.

In conclusion, FA may provide a mechanism for the tranfer of information during signalling at a number of different levels.

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Mechanisms and evolution in sexual selection. MJ Ryan, Dept. Zoology, University of Texas, Austin, TX, USA. Female mating preference is an important component of Darwin's theory of sexual selection. At the mechanistic level, we can view mating preferences as behavioral manifestations of sensory biases of females' that are exhibited when females perceive and compare male signals. We have been investigating the neural mechanisms underlying female mating preferences in frogs that are exhibited within populations, among populations, and among species. Also, when appropriate we have combined these studies with information of phylogenetic relationships to deduce the historical sequence of signal-receiver evolution. These patterns can allow us to evaluate various hypotheses concerning the evolution of female mating preferences. We suggest that sexual selection is best understood when combining information of neural mechanisms and evolutionary history together with the more usual approaches that utilizes population genetic models and field measures of reproductive success.

SUMMING UP

P. Bateson & M. Gomendio

Summing up

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The Workshop brought together research workers from many different disciplines to discuss the ways in which the study of functional issues and the study of the underlying mechanisms could be integrated. The scientific quality of the papers was very high and the discussion was good-tempered, constructive and well focused. From the stand-point of the organisers, the Workshop was an outstanding success (and we naturally hope that everybody who attended agrees with us). Despite a packed programme that started every day at 9.15 and on two of them continued until 18.45, the pattern of 20 minutes of prepared talk followed by 20 minutes of discussion worked well, thanks to the speakers' discipline and the co-operation of everybody. Behavioural biology differs from many other fields in that considerable time and effort is needed for discussion of conceptual issues. Molecular biology, for instance, does not possess such an elaborate theoretical background and tends to rely largely on the power of sophisticated laboratory techniques to uncover and describe the biological processes. For our field, the format of short talks and plenty of time for discussion was especially appropriate and many would have liked much more time for argument.

Inevitably, our own interests and friendships led to many omissions and what undoubtedly was an overwhelming bias towards the vertebrates. Nevertheless, the range of material was enormous and reflected what is perhaps both a weakness and a strength and of present day behavioural biology. The weakness is that replications in our field are unusual and parametric variation of important conditions influencing behaviour is not that common. The strength is that the new material constantly surprises and opens up new lines of research. We shall return to this point when considering where the subject might go.

It was remarkable to discover how people working on quite different aspects of animal behaviour had independently, but more or less simultaneously, come to the conclusion that the integration of the functional and causal approaches was the most fruitful way forward. Most participants felt that the powerful theoretical framework of behavioural ecology had lost some of the initial excitement in recent years and that the incorporation of the study of mechanisms would reinvigorate the field. Throughout the workshop it became clear that this combined approach could be applied successfully to many, if not all, aspects of the study of animal behaviour. There was an atmosphere of great excitement generated by the acknowledgement that the strict separation between the causal and the functional approach had been overcome, and that this was one of the few meetings (if not the first) where an effort to integrate the two approaches had not led to sterile discussions about old fashioned dichotomies or to the formation of two bands of people speaking different languages. The enthusiasm and the sense that something important was happening permeated the whole meeting.

Talk after talk showed the power of moving backwards and forwards between an understanding of how behaviour works and an understanding of how it evolved. The stream of ideas flowed both ways as we both hoped it would. Some speakers (beginning with the first, John Krebs) were intent on showing how an understanding of the contributions to the overall fitness of the animal helped to reach the goal of understanding how behaviour is organised. Others (ending with the last, Mike Ryan) showed how knowledge of behaviour and underlying neural mechanisms helps to reach the goal of understanding evolutionary processes.

Such intellectual tension as occurred in the meeting was primarily between the view that variation in behaviour is what matters most of all and the view that we should all be looking for universals. Of course, what this reflected was differences in research goals. If they had been pressed, most people at the Workshop would have agreed that they were more interested in one goal rather than the other, even though they would have disagreed about which was the most important one. However, it would be too crude to suggest that the broadening of behavioural biology has taken place because an all round approach to behaviour helps each research worker to get more easily to where they had always intended to go. A great many of those present at the Workshop quite simply took delight in the study of behaviour in all its diversity.

The manifest advantages of moving backwards and forwards between the how and why questions generated some concern that the clarity of Tinbergen's logical distinctions between the four problems of ethology would be lost (development, control, survival value and evolution). The consensus view of the Workshop seemed to be that lack of confusion about the distinctions was all the more necessary as the barriers between different compartments of knowledge became more permeable. That having been said, "mechanism" means different things to different people. The development and control of an individual's behaviour can both be investigated at many levels, the whole animal, the systems physiology and the molecular levels. Also as Robert Hinde has repeatedly emphasised, behaviour between individuals can be investigated in terms of interactions, relationships and social structures. For these reasons, we have to appreciate that, in addition to Tinbergen's distinction between the proximate questions of how behaviour develops and how it is controlled once fully assembled, clarity about differences between levels of organisation matters a lot.

On the ultimate side, the word "function" still causes confusion, even if we ignore its implications of purpose and the physiologists' usage in terms of the workings of a structure. Most people at the Workshop preferred to use "function" in the sense of current utility, namely that consequence of a behaviour pattern that will play the greatest part in enabling the animal to survive and reproduce itself in its present environment. This usage begs no questions about the historical origins of behaviour. Some people were plainly anxious about the distinction because current use sometimes provides the only evidence for historical process in studies of behaviour. Nevertheless, in our field as in others we have to accept that variation may arise from genetic drift and founder effects and we also have to be sensitive to the possibility that the behaviour pattern has been coopted from some other use or was a side-effect of an evolutionary process shaping another system. So, most felt that Tinbergen's distinction between survival value and historical process was well worth retaining.

The neo-Darwinian emphasis on the adaptation-creating aspects of the evolutionary process was a strong theme in sociobiology and behavioural ecology. It may have accounted for another semantic argument in the Workshop about the meaning of "constraint". Since one view has been that constraint refers to those factors that get in the way of a perfect match between behaviour and ecological conditions, it was thought by some of the more mechanistically inclined members of the Workshop to have a pejorative flavour, and is still used to play down the importance of mechanism. Many felt, though, that this was a residue of past compartmentalisation of the subject and, with the easier flow of ideas between "how" and "why" problems, these difficulties would soon disappear.

A more subtle language problem often arises when people with different interests and backgrounds start to interact. Unintended puns may lead to great confusion. We had several instances of this in the Workshop, namely over "conflict", "selection" and "active and passive choice". Genetic conflict of interest does not necessarily imply behavioural conflict. Evolutionary selection is clearly a different process from behavioural choice or, indeed, filtering of sperm by the female's reproductive tract. Finally, the distinction between active and passive evolutionary processes giving rise to the differential responding seen in mate choice does not necessarily map onto two types behavioural choice mechanism. Once these points have been made, problems of communication between scientists usually evaporate and, indeed, that seemed to be the case in the Workshop. Nevertheless, we need to be alert to such problems in the freshly re-integrated behavioural biology.

Some of the most interesting debates in the Workshop centred on the behavioural implications of evolutionary theory of parent-offspring conflict. These were not simply because of the punning use of "conflict". It became clear that most of the static ESS modelling of what might have happened in the course of evolution rested on great simplifications of behavioural process. When the flow of information between parent and offspring is taken into account, the evident disparity between what has been expected from evolutionary models and what has been found is much easier to understand. As the full complexity of the empirical observations was revealed, the theoreticians shook their heads in doubt about whether the modelling problems would be tractable. However, not everybody agreed and this may well be another area inviting application of the dynamic modelling techniques that John Krebs described for understanding foraging in sheep and Felicity Huntingford described for understanding salmon life-histories.

The discussion of parent-offspring communication tied into another hot topic in the Workshop, namely "honest signalling". Far from being manipulative, the signalling between parent and offspring may indicate real state and real needs. However, to be credible they have to carry a cost. The theory of honest signalling suggests that a signal has to be more expensive than is necessary for it to be unambiguous. Furthermore, the cost should relate to the nature of the need that is being honestly signalled. These ideas are still controversial, but they raise empirical questions about the character of signals that are different from those suggested by other ideas from evolutionary biology.

A hope was expressed at the beginning of the Workshop that our discussions might help us to formulate an agenda for the subject. Some hard-nosed (but sympathetic) biologists from other disciplines like to tell us that, if we really want to understand how behaviour works, we should focus our efforts on a few well chosen model animals, thereby concentrating effort and resources. Our pottering excursions down the country lanes of animal diversity are luxuries that we can no longer afford. We should all get on to the motorways and drive as fast and as furiously as we can towards the goal of describing the universal principles that underlie the organisation of behaviour. Such tough-minded advice undoubtedly has some force, but it clearly does not apply to those people wishing to uncover evolutionary principles, for whom the study of diversity is crucial. Concentrating effort and resources on a few model species would completely miss the point of their work.

Even for those primarily interested in how behaviour develops and is integrated, the advice from fellow biologists has to be balanced against various pressures in the opposite direction. For a start, some important general features of behavioural organisation may simply not be tackled tractably in a particular model animal. This has been obvious enough in genetics and development biology where focus on particular animals such as *Drosophila* has been powerful, but would have been too restrictive if these had been the only ones to have been studied. Secondly, the motivating effects of being exposed to different aspects of a subject should not be underestimated. Nevertheless, it is certainly the case that we have to think seriously about the trade-offs that are required in order to make most rapid progress in the field.

We also have to blow our own trumpets. If we fail to communicate our own sense of excitement about the coherence and promise of the subject, we have only ourselves to blame if others, who advertise themselves more aggressively, corner the available funds for research. Commitment to our own subject does not require us all to become scientific politicians, copy-writers or commercial travellers. What is required is considerable co-operation between all those who are active in the field in assembling a good case.

The Fundacion Juan March provided a perfect setting for the Workshop. It is one of the those rare institutions where art and science, co-exist in harmony. What better place for a discussion of ideas? Ideas provide the motor for understanding and we are deeply grateful to the foundation for its generosity and foresight in lubricating the process.

LIST OF INVITED SPEAKERS

Workshop on

BEHAVIOURAL MECHANISMS IN EVOLUTIONARY PERSPECTIVE

List of Invited Speakers

J.R. Alberts	*Research and the University Graduate School, Indiana University, Bryan Hall 104, Bloomington, IN. 47405 (USA)* *Tel.: 812 855 33 09* *Fax : 812 855 21 00*
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LIST OF PARTICIPANTS

Workshop on

BEHAVIOURAL MECHANISMS IN EVOLUTIONARY PERSPECTIVE

List of Participants

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Texts published in the
SERIE UNIVERSITARIA
by the
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concerning workshops and courses organized within the Plan for International Meetings on Biology (1989-1991)

246 **Workshop on Tolerance: Mechanisms and implications.**
Organized by P. Marrack and C. Martínez-A. Lectures by H. von Boehmer, J. W. Kappler, C. Martínez-A., H. Waldmann, N. Le Douarin, J. Sprent, P. Matzinger, R. H. Schwartz, M. Weigert, A. Coutinho, C. C. Goodnow, A. L. DeFranco and P. Marrack.

247 **Workshop on Pathogenesis-related Proteins in Plants.**
Organized by V. Conejero and L. C. Van Loon. Lectures by L. C. Van Loon, R. Fraser, J. F. Antoniw, M. Legrand, Y. Ohashi, F. Meins, T. Boller, V. Conejero, C. A. Ryan, D. F. Klessig, J. F. Bol, A. Leyva and F. García-Olmedo.

248 Beato, M.:
Course on DNA - Protein Interaction.

249 **Workshop on Molecular Diagnosis of Cancer.**
Organized by M. Perucho and P. García Barreno. Lectures by F. McCormick, A. Pellicer, J. L. Bos, M. Perucho, R. A. Weinberg, E. Harlow, E. R. Fearon, M. Schwab, F. W. Alt, R. Dalla Favera, P. E. Reddy, E. M. de Villiers, D. Slamon, I. B. Roninson, J. Groffen and M. Barbacid.

251 **Lecture Course on Approaches to Plant Development.**
Organized by P. Puigdoménech and T. Nelson. Lectures by I. Sussex, R. S. Poethig, M. Delseny, M. Freeling, S. C. de Vries, J. H. Rothman, J. Modolell, F. Salamini, M. A. Estelle, J. M. Martínez Zapater, A. Spena, P. J. J. Hooykaas, T. Nelson, P. Puigdoménech and M. Pagès.

252 **Curso Experimental de Electroforesis Bidimensional de Alta Resolución.**
Organizado por Juan F. Santarén. Seminarios por Julio E. Celis, James I. Garrels, Joël Vandekerckhove, Juan F. Santarén y Rosa Assiego.

253 **Workshop on Genome Expression and Pathogenesis of Plant RNA Viruses.**
Organized by F. García-Arenal and P. Palukaitis. Lectures by D. Baulcome, R. N. Beachy, G. Boccardo, J. Bol, G. Bruening, J. Burgyan, J. R. Díaz Ruiz, W. G. Dougherty, F. García-Arenal, W. L. Gerlach, A. L. Haenni, E. M. J. Jaspars, D. L. Nuss, P. Palukaitis, Y. Watanabe and M. Zaitlin.

254 **Advanced Course on Biochemistry and Genetics of Yeast.**
Organized by C. Gancedo, J. M. Gancedo, M. A. Delgado and I. L Calderón.

255 **Workshop on The Reference Points in Evolution.**
Organized by P. Alberch and G. A. Dover. Lectures by P. Alberch, P. Bateson, R. J. Britten, B. C. Clarke, S. Conway Morris, G. A. Dover, G. M. Edelman, R. Flavell, A. Fontdevila, A. García-Bellido, G. L. G. Miklos, C. Milstein, A. Moya, G. B. Müller, G. Oster, M. De Renzi, A. Seilacher, S. Stearns, E. S. Vrba, G. P Wagner, D. B. Wake and A. Wilson.

256 **Workshop on Chromatin Structure and Gene Expression.**
Organized by F. Azorín, M. Beato and A. A. Travers. Lectures by F. Azorín, M. Beato, H. Cedar, R. Chalkley, M. E. A. Churchill, D. Clark, C. Crane-Robinson, J. A. Dabán, S. C. R. Elgin, M. Grunstein, G. L. Hager, W. Hörz, T. Koller, U. K. Laemmli, E. Di Mauro, D. Rhodes, T. J. Richmond, A. Ruiz-Carrillo, R. T. Simpson, A. E. Sippel, J. M. Sogo, F. Thoma, A. A. Travers, J. Workman, O. Wrange and C. Wu.

257 **Lecture Course on Polyamines as modulators of Plant Development.** Organized by A. W. Galston and A. F. Tiburcio. Lectures by N. Bagni, J. A. Creus, E. B. Dumbroff, H. E. Flores, A. W. Galston, J. Martin-Tanguy, D. Serafini-Fracassini, R. D. Slocum, T. A. Smith and A. F. Tiburcio.

258 **Workshop on Flower Development.** Organized by H. Saedler, J. P. Beltrán and J. Paz Ares. Lectures by P. Albersheim, J. P. Beltrán, E. Coen, G. W. Haughn, J. Leemans, E. Lifschitz, C. Martin, J. M. Martínez-Zapater, E. M. Meyerowitz, J. Paz-Ares, H. Saedler, C. P. Scutt, H. Sommer, R. D. Thompson and K. Tran Thahn Van.

259 **Workshop on Transcription and Replication of Negative Strand RNA Viruses.** Organized by D. Kolakofsky and J. Ortín. Lectures by A. K. Banerjee, M. A. Billeter, P. Collins, M. T. Franze-Fernández, A. J. Hay, A. Ishihama, D. Kolakofsky, R. M. Krug, J. A. Melero, S. A. Moyer, J. Ortín, P. Palese, R. G. Paterson, A. Portela, M. Schubert, D. F. Summers, N. Tordo and G. W. Wertz.

260 **Lecture Course Molecular Biology of the Rhizobium-Legume Symbiosis.** Organized by T. Ruiz-Argüeso. Lectures by T. Bisseling, P. Boistard, J. A. Downie, D. W. Emerich, J. Kijne, J. Olivares, T. Ruiz-Argüeso, F. Sánchez and H. P. Spaink.

261 **Workshop The Regulation of Translation in Animal Virus-Infected Cells.** Organized by N. Sonenberg and L. Carrasco. Lectures by V. Agol, R. Bablanian, L. Carrasco , M. J. Clemens, E. Ehrenfeld, D. Etchison, R. F. Garry, J. W. B. Hershey, A. G. Hovanessian, R. J. Jackson, M. G. Katze, M. B. Mathews, W. C. Merrick, D. J. Rowlands, P. Sarnow, R. J. Schneider, A. J. Shatkin, N. Sonenberg, H. O. Voorma and E. Wimmer.

263 **Lecture Course on the Polymerase Chain Reaction.** Organized by M. Perucho and E. Martínez-Salas. Lectures by D. Gelfand, K. Hayashi, H. H. Kazazian, E. Martínez-Salas, M. Mc Clelland, K. B. Mullis, C. Oste, M. Perucho and J. Sninsky.

264 **Workshop on Yeast Transport and Energetics.** Organized by A. Rodríguez-Navarro and R. Lagunas. Lectures by M. R. Chevallier, A. A. Eddy, Y. Eilam, G. F. Fuhrmann, A. Goffeau, M. Höfer, A. Kotyk, D. Kuschmitz, R. Lagunas, C. Leão, L. A. Okorokov, A. Peña, J. Ramos, A. Rodríguez-Navarro, W. A. Scheffers and J. M. Thevelein

265 **Workshop on Adhesion Receptors in the Immune System.** Organized by T. A. Springer and F. Sánchez-Madrid. Lectures by S. J. Burakoff, A. L. Corbi-López, C. Figdor, B. Furie, J. C. Gutiérrez-Ramos, A. Hamann, N. Hogg, L. Lasky, R. R. Lobb, J. A. López de Castro, B. Malissen, P. Moingeon, K. Okumura, J. C. Paulson, F. Sánchez-Madrid, S. Shaw, T. A. Springer, T. F. Tedder and A. F. Williams.

266 **Workshop on Innovations on Proteases and their Inhibitors: Fundamental and Applied Aspects.** Organized by F. X. Avilés. Lectures by T. L. Blundell, W. Bode, P. Carbonero, R. W.Carrell, C. S. Craik, T. E. Creighton, E. W. Davie, L. D. Fricker, H. Fritz, R. Huber, J. Kenny, H. Neurath, A. Puigserver, C. A. Ryan, J. J. Sánchez-Serrano, S. Shaltiel, R. L. Stevens, K. Suzuki, V. Turk, J. Vendrell and K. Wüthrich.

267 **Workshop on Role of Glycosyl-Phosphatidylinositol in Cell Signalling.** Organized by J. M. Mato and J. Larner. Lectures by M. V. Chao, R. V. Farese, J. E. Felíu, G. N. Gaulton, H. U. Häring, C. Jacquemin, J. Larner, M. G. Low, M. Martín Lomas, J. M. Mato, E. Rodríguez-Boulan, G. Romero, G. Rougon, A. R. Saltiel, P. Strålfors and I. Varela-Nieto.

268 **Workshop on Salt Tolerance in Microorganisms and Plants: Physiological and Molecular Aspects.** Organized by R. Serrano and J. A. Pintor-

Toro. Lectures by L. Adler, E. Blumwald, V. Conejero, W. Epstein, R. F. Gaber, P. M. Hasegawa, C. F. Higgins, C. J. Lamb, A. Läuchli, U. Lüttge, E. Padan, M. Pagès, U. Pick, J. A. Pintor-Toro, R. S. Quatrano, L. Reinhold, A. Rodríguez-Navarro, R. Serrano and R. G. Wyn Jones.

269 **Workshop on Neural Control of Movement in Vertebrates.**
Organized by R. Baker and J. M. Delgado-García. Lectures by C. Acuña, R. Baker, A. H. Bass, A. Berthoz, A. L. Bianchi, J. R. Bloedel, W. Buño, R. E. Burke, R. Caminiti, G. Cheron, J. M. Delgado-García, E. E. Fetz, R. Gallego, S. Grillner, D. Guitton, S. M. Highstein, F. Mora, F. J. Rubia Vila, Y. Shinoda, M. Steriade and P. L. Strick.

Texts published by the
CENTRE FOR INTERNATIONAL MEETINGS ON BIOLOGY

1 **Workshop on What do Nociceptors Tell the Brain?**
Organized by C. Belmonte and F. Cerveró. Lectures by C. Belmonte, G. J. Bennet, J. N. Campbell, F. Cerveró, A. W. Duggan, J. Gallar, H. O. Handwerker, M. Koltzenburg, R. H. LaMotte, R. A. Meyer, J. Ochoa, E. R. Perl, H. P. Rang, P. W. Reeh, H. G. Schaible, R. F. Schmidt, J. Szolcsányi, E. Torebjörk and W. D. Willis Jr.

2 **Workshop on DNA Structure and Protein Recognition.**
Organized by A. Klug and J. A. Subirana. Lectures by F. Azorín, D. M. Crothers, R. E. Dickerson, M. D. Frank-Kamenetskii, C. W. Hilbers, R. Kaptein, D. Moras, D. Rhodes, W. Saenger, M. Salas, P. B. Sigler, L. Kohlstaedt, J. A. Subirana, D. Suck, A. Travers and J. C. Wang.

3 **Lecture Course on Palaeobiology: Preparing for the Twenty-First Century.**
Organized by F. Álvarez and S. Conway Morris. Lectures by F. Álvarez, S. Conway Morris, B. Runnegar, A. Seilacher and R. A. Spicer.

4 **Workshop on The Past and the Future of Zea Mays.**
Organized by B. Burr, L. Herrera-Estrella and P. Puigdoménech. Lectures by P. Arruda, J. L. Bennetzen, S. P. Briggs, B. Burr, J. Doebley, H. K. Dooner, M. Fromm, G. Gavazzi, C. Gigot, S. Hake, L. Herrera-Estrella, D. A. Hoisington, J. Kermicle, M. Motto, T. Nelson, G. Neuhaus, P. Puigdoménech, H. Saedler, V. Szabo and A. Viotti.

5 **Workshop on Structure of the Major Histocompatibility complex.**
Organized by A. Arnáiz-Villena and P. Parham. Lectures by A. Arnaiz-Villena, R. E. Bontrop, F. M. Brodsky, R. D. Campbell, E. J. Collins, P. Cresswell, M. Edidin, H. Erlich, L. Flaherty, F. Garrido, R. Germain, T. H. Hansen, G. J. Hämmerling, J. Klein, J. A. López de Castro, A. McMichael, P. Parham, P. Stastny, P. Travers and J. Trowsdale.

The Centre for International Meetings on Biology
has been created within the
Instituto Juan March de Estudios e Investigaciones,
a private foundation which complements the work
of the *Fundación Juan March* (established in 1955)
as an entity specialized in scientific activities
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The Centre's initiatives stem from the Plan
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supported by the *Fundación Juan March*.
A total of 30 meetings and 3 Juan March Lecture
Cycles, all dealing with a wide range of subjects
of biological interest, were organized between
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The Centre endeavours to actively and
sistematically promote cooperation among Spanish
and foreign scientists working in the field of Biology,
through the organization of Lecture
and Experimental Courses, Workshops, Seminars,
Symposia and the Juan March Lectures on Biology.

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