On the communication of well-being

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Abstract. The form that any communicatory exchange takes would depend on the extent to which the interests of the signaller and the recipient are at variance. Where such interests coincide, i.e. in cases of mutualism, the signals may be conspicuous when an immediate response is favoured, but rather subtle and variable otherwise. Over 80 % of the events of tactile communication that we have noted in our study of the social behaviour of free ranging groups of tame elephants appear to belong to this latter category. On Smith's standard classification, they can only be classified as 'associative', related to remaining in the company of another individual. However, such signals are commoner by a factor of 20–100 amongst elephant calves and their mothers and allomothers when compared to exchanges between adult cows. We suggest that the function of these signals is mutual monitoring of the state of well being amongst related individuals. The considerable degree of altruistic behaviour displayed in social groups, such as those of elephants is now believed to subserve the function of enhancing the inclusive fitness of the individuals concerned. We explore a mathematical model of exchange of social aid which suggests that animals in social groups may enhance their inclusive fitness further by adjusting the amount of social aid exchanged in relation to the state of well being of the donor as well as the recipient. Our model further suggests that optimal social aid depends on the state of well being in a complex fashion making it difficult for the recipient to deceive the donor so as to extract more aid. We therefore expect that by and large honest communication of the state of well being would be characteristic of the higher social animals. Such communication would be based on normal physiological changes consequent on a change in well being. Thus animals with a superior degree of well being would take postures conducive to greater activity, would be more receptive to sensory inputs and may also shift the balance of production of various metabolites. This monitoring of the well being has greatly advanced in the human species and may be at the base of the elaborate health care amongst human societies.

Keywords. Communication; well-being; kin selection; elephants.

1. Introduction

Animals, whether they be lowly soil amoebae or highly evolved elephants, are creatures on the move. For them success depends on being alert to what is happening around them. They have therefore evolved a variety of sense organs to receive signals of relevance to their own welfare from the environment. Such signals may be picked up opportunistically, regardless of the interests of the signaller. Thus many species of soil amoebae possess on their body surface receptors for derivatives of folic acid. These chemical compounds are involved in the biosynthesis of purines and pyrimidines, the basic building blocks of nucleic acids that are essential for every living organism. It turns out that they leak out of the bodies of bacteria grazed on by soil amoebae. Soil amoebae then employ the folic acid derivatives as signals to locate their prey, moving up the gradient of concentration. This is thus an example of interception of a signal against

the interest of the signaller. In another paper in this issue Stanley Rand will add another, that of predatory bats homing on to male frogs calling to keep out the other males and to attract the females.

2. Eavesdropping

In general, we can classify signals into 4 categories depending on whether the signaller benefits or suffers from the recipient receiving it, and on whether the recipient benefits or suffers from acting on it (Wiley 1983).

		Signaller	
R		Benefits	Suffers
e			
c	Benefits	Mutualism	Eavesdropping
i			
p	Suffers	Deceit	Spite
i			
e			
n			
t			

The genetic interests of the predatory soil amoebae and their bacterial prey are obviously divergent, making the use of folic acid derivatives to locate them an example of eavesdropping. But two of the species of soil amoebae *Dictyolstelium lacteum* and *D. minutum* use folic acid derivatives as communicatory signals in quite another context— to attract each other. These soil amoebae multiply by binary fission, feeding on bacteria in their vegetative phase. When the food supply runs out, members of a clone come together to form a many celled creature called the slug. Some cells of this slug forego reproduction to form a stalk, while other cells turn into spores which disperse and may enter again into the vegetative phase if they encounter a favourable environment.

In terms of our classification above, some of the soil amoebae that are thus attracted by the signal suffer, since they forego their chances of reproduction to form the stalk, while others benefit, since they form spores which retain the possibility of future reproduction. In the process of aggregation of soil amoebae, all cells produce the signal and all cells receive it. Is this communicatory episode then an example of deceit by future spore cells signalling the future stalk cells, or eavesdropping on the signal of future stalk cells by the future spore cells?

3. Altruism

A closer look suggests that in fact it is neither. The soil amoebae attracting each other are all members of a clone, and therefore genetically identical. The assumption of the role of stalk cells by some of the amoebae is an example of altruistic behaviour through kin selection. As Hamilton (1964) has shown, natural selection will favour such behaviour so long as:

Cost to the altruist < Benefit to the recipient x kinship coefficient

where the kinship coefficient is the proportion of genes shared by virtue of common ancestry. Members of a soil amoebae clone will have a kinship coefficient of 1. Suppose now that a proportion x of them sacrifices a chance to reproduce by forming a stalk; leaving $(1 - x)$ to reproduce. Then this behaviour would be favoured if raising on a stalk improves the chance of survival of a spore by a factor greater than $\dfrac{1}{1 - x}$.

There are good reasons to believe that this is in fact so. In that case the genetic interests of all the soil amoebae that are attracted to each other by signals employing folic acid derivatives are served by producing and responding to the signal. This is then an example of mutualism in our classification of communicatory systems. Vidyanand Nanjundiah discusses these fascinating organisms in greater detail in another paper in this issue.

4. Information and manipulation

We have thus far looked at two extremes—total divergence of genetic interests as with bacteria and their predators, and total congruence of genetic interests as with members of a clone of soil amoebae. There would however be many examples of only a partial congruence of genetic interests, resulting in a rich structure of animal communication (Dawkins and Krebs 1978; Krebs and Dawkins 1984).

Consider for a moment the call of male frogs. It is in the interest of female frogs to locate a mate, preferably a mate that will contribute qualities that will help the offspring succeed in life. It is likely that the biggest available male of their own species will be their best choice. It will therefore be in the interest of the females to be able to derive information on the size of the calling male from its call. On the contrary, it will be in the genetic interest of every male to misinform the females, conveying that the signaller is much bigger than in fact it is. We could then consider the information being transmitted during any communicatory exchange under 3 components:

	Signaller	
True information sought to be transmitted in mutual interest	True information sought to be suppressed	False information sought to be transmitted
α	β	γ
True information sought to be received in mutual interest	True information sought to be received against the interest of signaller	False information sought to be discounted in interest of the recipient
	Recipient	

Any communicatory exchange could be characterized usefully by the relative values of α, β and γ. In the case of bacteria and amoebae β dominates, the bacteria would rather produce no signal if it were metabolically easily possible; while α dominates in case of members of a clone of soil amoebae attracting each other. With male frogs calling to attract females, γ must assume significance with males evolutionarily favoured to convey an exaggerated impression of their size and females favoured to discount any

such bluff. As Wiley (1983) and Krebs and Dawkins (1984) have argued this should lead to the evolution of rather stereotyped, repetitive and unbluffable signals. These are the conspicuous displays that have so attracted students of animal behaviour.

5. Kinship discrimination

It appears reasonable to conclude that signals would tend to be conspicuous because of their stereotype and repetition when γ is significant, and rather inconspicuous when β dominates. In the context of mutualism, when α dominates, they may be conspicuous when immediate response is favoured, as with soil amoebae attracting each other. In other mutualistic contexts, however, the signals are expected to be rather subtle and variable and therefore escape the attention of the ethologist (Krebs and Dawkins 1984). One such context is that of discrimination of kinship level. This could be important in social animals, for as J B S Haldane is supposed to have said—he would be evolutionarily favoured to lay down his life to save two full brothers from drowning; but if it were only first cousins he must save at least 8 of them for this to make genetic sense. This is because while full brothers have a kinship coefficient of 1/2, first cousins share only 1/8 of their genes by virtue of common ancestry.

Discrimination of levels of kinship should therefore be important in social animals. But it may be based on very subtle and variable cues and it is only now that we are finding out that in some social insects individuals can discriminate kinship levels based on chemical signals, even in the absence of individual recognition. This is a topic that will be reviewed in detail in another paper in this issue by Raghavendra Gadagkar.

Amongst higher animals such as mammals on the other hand, sociality is based on individual recognition. Many mammals use chemical signals in the form of ratios of several compounds for this purpose. This individual recognition coupled with ties established from birth onwards between the mother and the young must permit a fine tuning of social behaviour in higher mammals such as elephants.

6. Elephant societies

Along with Dr P Vijayakumaran Nair of Kerala Forest Research Institute, we have investigated the structure of social behaviour in the Asiatic Elephant (*Elephas maximus*). For this purpose we used tame elephants maintained in elephant camps in South Indian forests. All the adults were caught from the wild in the same or nearby forests and the tame elephants were left for grazing in their natural habitat. These tame elephants often mingled with wild herds when thus left free. In fact all the calves born in captivity were sired by wild tuskers. We observed these elephants over a period of 23 months between February 1975 to March 1976 and January 1978 to August 1979. The total amount of time spent in the field recording behavioural details spanned 645 hr. Our parallel, but less detailed observations on the wild elephants confirmed that the behaviour patterns within the artificially constituted social groups of tame elephants closely resembled those of wild elephants. In particular, adult females reacted to calves of other females as did wild females to calves of other females in their herd. Under natural conditions, of course, the several adult females in a single herd are related to each other as mother-daughter-half-sister-aunts-cousins (Douglas Hamilton 1972).

The glue that holds the elephant society together is evidently the protection and nurture of calves. These herbivores would only reduce their feeding efficiency by being together; and the adults can resist any predation by themselves. The calves, however, are still susceptible to predation, and in fact an elephant calf fell prey to a tiger in Bandipur during our study period. Adult female elephants therefore stay together to help protect each other's calves, which under natural conditions have kinship coefficients of 1/2–1/16 with the adult females. The adult males wander from herd to herd and can have little clue as to which calves they have sired. As expected, they play no role in helping the calves.

The social group of elephants therefore comprises related adult females with their young sons, daughters, cousins, nephews and nieces. The calves station themselves in between adult females who run to them on slightest alarm. The adult females stand guard over the calves when the latter sleep, and also suckle them if they have no suckling calves of their own. Elephants are thus model aunts or allomothers. The role of calves in holding these females together was strikingly brought out when the only calf with 3 adult females of Bandipur Tiger Reserve was removed for weaning. As soon as the calf was gone, the cows started grazing separately by themselves (Gadgil and Nair 1984).

7. Communication amongst elephants

Elephants have poor vision and do not seem to base much of their·social communication on visual signals. We have little information on the extent to which they depend on chemical signals except that they seem to base individual recognition on it. They do use vocal signals, especially to communicate alarm and aggression. Tactile communication however seems to be the dominant mode of communication, especially where the calves are involved. These tactile contacts are largely initiated by the calf towards mother or allomother. Thus in a group of 3 adult females and a calf of less than 6 months of age in Bandipur Tiger Reserve the calf touched the mother and one of the allomothers at a rate of about 4 times in 10 min while it touched a second allomother at a lower rate of once in 10 min. The mother touched the calf at the rate of once in 7 min, the first allomother did so at the rate of once in 20 min, while the second allomother touched the calf at the rate of once in 50 min. The adults touched each other at low rates ranging from once in 50 to once in 300 min.

A question of considerable significance is the function of the different acts of communication. In some cases the function is evident as when a calf follows a contact by suckling or rushes to the mother when the latter sounds an alarm call. A remarkable result however is that in the vast majority of cases, of the order of 80 %, no such clear cut immediate function can be attached to a communicatory exchange. The intriguing question therefore is this: what are the adult elephant, cows and calves conveying to each other most of the time?

I believe that our failure to assign any obvious function to the bulk of these communicatory exchanges is due to the fact that it does not subserve any immediate need. Consequently, in this mutualistic system the signals, as expected, are inconspicuous and variable. On Smith's (1977) standard classification they can be only classified as 'associative', related to remaining in the company of another individual. But then elephant females remain in company with each other often for their whole lives.

Nevertheless the adult females have a far lower frequency of tactile communication amongst themselves – by a factor of 20–100 than females and calves.

8. Monitoring well-being

We therefore suggest that there is an additional function of communication in case of higher social animals like the elephants that has not so far been clearly identified; this is the monitoring of the state of well-being of the young by related adults.

To understand why such communication of well-being could be favoured during the course of evolution, we have to go back to Hamilton's inequality:
An altruistic act will be favoured if:

Cost to altruistic donor <

Benefit to recipient x kinship coefficient
between donor and
recipient.

A superficial examination of this statement suggests the following paradox: the kinship coefficient between a mother and her off-spring and between two full sisters is the same, namely 1/2. Nevertheless, a female mammal displays much greater level of altruistic behaviour towards her offsprings than towards her sisters, or towards her mother. The resolution of this paradox lies in recognising that the costs and benefits of a given altruistic act will differ substantially depending on the identity of the actors involved. These benefits and costs must be measured as marginal changes in the reproductive value of an individual as a result of a given social act. Since social aid will often make greater difference to the chances of survival and future reproduction of a young offspring than that of a grown sister or an old mother, a female mammal will be generally favoured by natural selection to behave far more altruistically towards her offspring rather than a sister or a mother. This need not always hold, of course, and one needs a better defined model to explore this proposition further. Such a model cannot of course reflect all the complexities of the real world; that would be too cumbersome to handle. Rather, the model we develop should be rich enough to reflect the essentials but simple enough to handle and be interpretable.

9. Modelling social interactions

In such a model the physiological status of the interacting individuals could be specified by 3 parameters: the ability to convert resources into somatic or reproductive growth, α, the cost of maintenance, β and the extent to which physical growth has been completed and independent abilities to gather resources achieved S. The extent of favourability of environment is reflected in a parameter F. Let us assume that each individual i has at its disposal some resources taken to be proportional to $S_i F$ for maintenance and growth. Of these it retains a fraction ϕ_{ii} for its own use and donates a fraction ϕ_{ij} to the jth individual. Then the total amount of resources available to it, θ_i, is given by

$$\theta_i = \sum_j S_j F \phi_{ji}$$

The marginal change in fitness or the reproductive value of the ith individual, ΔW_i

depends on the change in S_i, i.e. ΔS_i. We take:

$$\Delta S_i = S_i(\alpha(1 - S_i)(1 - e^{-\theta_i/S_i\beta_i}) - \beta_i e^{-\theta_i/\beta_i S_i})$$

and W_i is given by:

$$W_i = 1 - e^{-3(S_i + \Delta S_i)}.$$

Hamilton's (1964) extension of the genetical theory of natural selection tells us that each individual will be so programmed as to maximise its inclusive fitness

$$H_i = \sum_j W_j \gamma_{ij}$$

where γ_{ij} is the kinship coefficient between i and j.

We can therefore determine for any given α_i, β_i, S_i, F values the ϕ_{ij} that will tend to maximize the inclusive fitness of each individual involved. The problem is made complex by the fact that the optimal allocation of resources for an individual i depends on the allocation strategies adopted by other individuals. In such an interactive population, evidently the allocation strategy ϕ_{ij} of the ith individual will be such that the inclusive fitness of this individual is maximum for the existing strategies $\phi_{kj}(k \neq i)$ of other individuals. We know that such a point exists, and have a working algorithm for determining this matrix for the case of two interacting individuals, say the mother(1) and the offspring(2).

In this simple case of two individuals, it can be shown that ϕ_{ii} is always 1 for atleast one of the two individuals; i.e., one of the individuals may be a donor and the other the recipient keeping all of its own resources to itself, or both may keep all their resources to themselves. We naturally identify the donor in our model with the mother(1), and the recipient with the offspring(2). Our problem then is to determine the optimal level of maternal investment, i.e., social aid ϕ_{12} from the mother to the offspring.

10. Optimal maternal investment

There are two immediately interesting results of our model. The first is that optimal maternal investment is much more sensitive in variation to the offspring's cost of maintenance β_2, extent of development completed S_2, and the extent of favourability of the environment F, than it is to efficiency of growth α_2 (figure 1). This result is probably related to the fact that the first 3 parameters appear in the exponential term of our specific model. Secondly, we find that the optimal level of maternal investment need not vary monotonically with the value of variables specifying offspring's state. That is to say the mother will not necessarily provide more and more maternal care as offspring's apparent needs increase. This is because the optimal level of maternal investment depends on the extent to which an offspring can enhance its reproductive value by receiving such help. An offspring not in much need can make little use of aid; at the same time, an offspring too much in need may also be a bad investment. We are reminded of Kafka's story 'Metamorphosis' in which the son of the family is turned into a cockroach. Initially, while there is hope that he will turn back into man much help is lavished on him. But as time goes on and he remains an insect, he is neglected and ultimately allowed to die. There will thus be an intermediate level of need by offspring
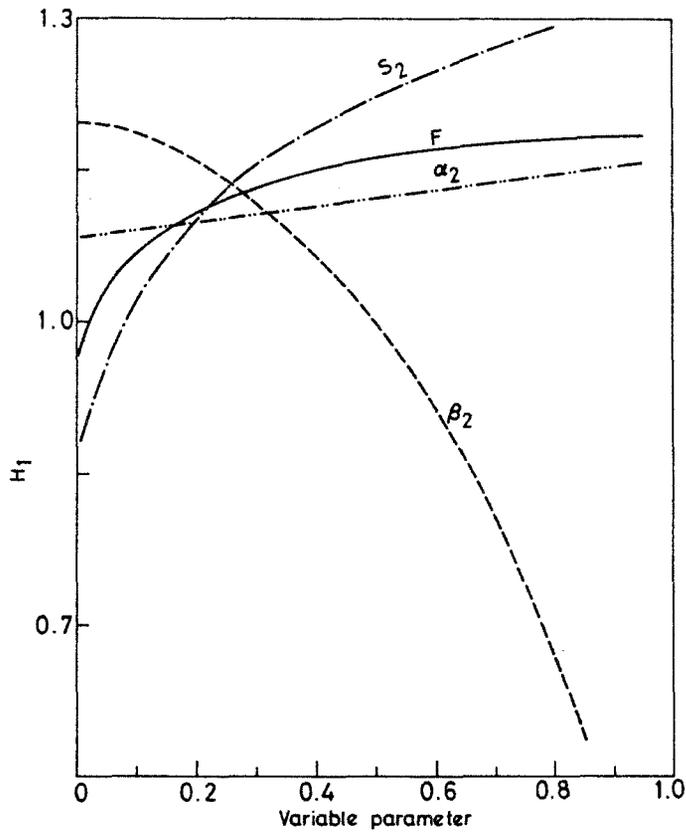
Figure 1. Inclusive fitness of mother (H_1) as a function of variation in α_2, β_2 S_2 or F varying one parameter at a time. The fixed values of other parameters are taken to be $\alpha_1 = 0.6, \alpha_2 = 0.1$, $\beta_1 = 0.4, \beta_2 = 0.4, S_1 = 1, S_2 = 0.15, F = 0.1$.

which will attract maximal investment. This level will also depend on mother's condition (figures 2 and 3).

What are the implications of these results for our central theme, the value of communication of well-being? A mother can be programmed to fix the level of maternal investment at the value which will maximize her inclusive fitness, if information on the offspring's state is available to her. In the absence of such information, she will either make too much or too little maternal investment and thereby suffer a decline in her inclusive fitness. Our model shows that the availability of information relating to the offspring's well-being can indeed make a significant difference in mother's inclusive fitness. Mothers of highly social species and with a nervous system developed enough to make possible fine adjustments in maternal care should therefore be favoured evolutionarily to look for information on the well-being of her offspring.

11. Mother-infant conflict

Trivers (1974) points to a very intriguing complication that must arise in this context due to the fact that since an offspring shares only 1/2 of its genes with its mother, its
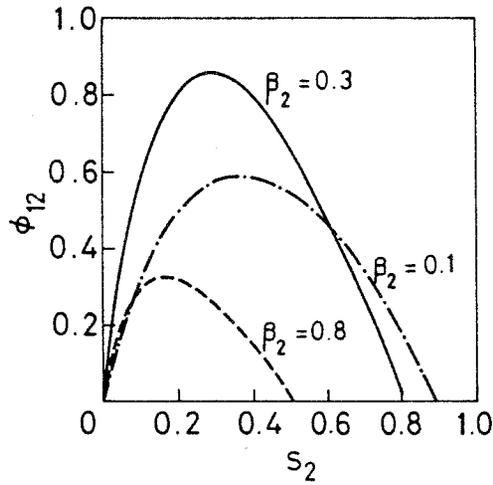
Figure 2. Optimal maternal investment, ϕ_{12} as a function of S_2 for different values of β_2. The values of other parameters are $\alpha_1 = 0.6$, $\alpha_2 = 0.6$, $\beta_1 = 0.4$, $S_1 = 1$, $F = 0.1$.
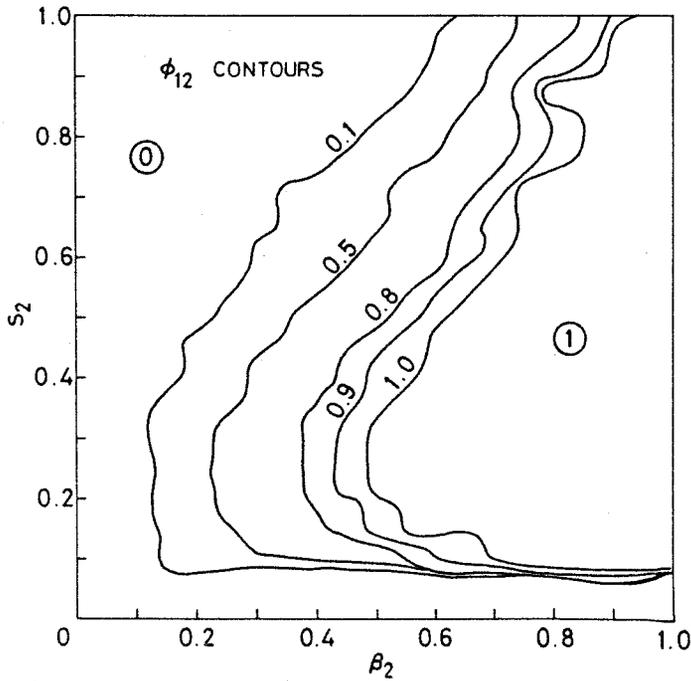

Figure 3. Contours of optimal maternal investment ϕ_{12} as a function of S_2 and β_2. The values of other parameters are $\alpha_1 = 0.6$, $\alpha_2 = 0.6$, $\beta_1 = 0.4$, $S_1 = 1$ and $F = 0.1$.

genetic interests will diverge, though within limits, from those of its mother. It would then be expected to try to extract a higher level of maternal investment ϕ_{12}, then the mother would be selected to offer. Hence the weaning conflict in mammals with the

mother attempting to stop suckling and the offspring attempting to continue doing so at a certain age. In context of the problem of our interest, the offspring can gain in its inclusive fitness by miscommunicating to the mother the value of its well-being so as to extract a higher level of ϕ_{12}. Our model has a very interesting result bearing on this issue, namely that optimal ϕ_{12} that the mother would be programmed to adopt does not change in a simple fashion with parameters specifying the offspring's condition (figures 2 and 3). That is, a mother will not always increase her level of maternal investment if the offspring's condition is better or worse. Under certain conditions she will increase it, under others decrease it. There is therefore no simple strategy available to the offspring of misinforming its mother of its own level of well-being so as to prompt her to enhance the level of maternal investment. Hence natural selection would tend to disfavour any manipulation of information relating to its own state from the offspring to its mother (figure 4).

Our enquiry thus suggests that atleast in higher animals with a well developed nervous system and high levels of maternal care such as elephants and human beings, communication of well-being must be a significant component of social communication.

12. Communication of well-being

We began by noting that soil amoebae use folic acid derivatives which are normal products of bacterial metabolism as signals to locate their prey, and further that these have been elaborated to serve as signals for aggregation in some species of soil amoebae. Evolution has thus opportunistically siezed upon normal physiology of animals from which to elaborate communicatory signals. Signals communicating well-being must
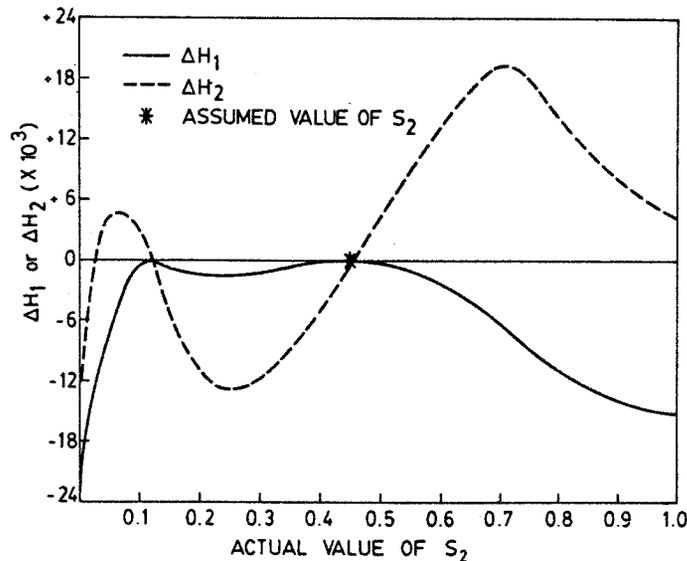
Figure 4. Change in inclusive fitness of mother (ΔH_1) or offspring (ΔH_2) when optimal maternal investment is based assuming S_2 to be 0·45, but is in fact different. The values of other parameters are $\alpha_1 = 0·6$, $\alpha_2 = 0·6$, $\beta_1 = 0·4$, $S_1 = 1$, $F = 0·1$.

similarly relate to normal physiological changes in an offspring brought about by a change in its state of well being. An animal must adjust its metabolism, activity level and behavioural patterns to its level of well being, though this problem does not appear to have been specifically investigated with this view point. Coming back to the elephants, Dr V Krishnamurthy of Tamilnadu Forest Department who has handled elephants for 30 years as a Veterinarian, tells us that a male elephant will come into musth only if he is given light work and fed well and is in excellent physical condition. A male elephant's physiology thus shifts into this mode only when its state of well-being is high. There must be other chemical substances that an elephant calf, say, will start producing in large quantities only when it is in good health; shifting to others as its health declines. An elephant mother may continually monitor the state of well being of its offsprings through monitoring such chemical signals.

The state of well being of an individual will also be reflected in its activity level. Andrew (1972) talks of an exertion/immobility continuum along which an individual mammal may be placed. We expect it to move towards greater exertion with an improvement in its state of well being. This will be reflected in its posture; thus in horses being more active leads to a high postural tonus with a raising of the tail. An active mammal also tends to adopt postures which would lead to a loss of heat, an inactive one curled up postures designed to conserve heat. We may also expect more active animals to be much more receptive to sensory cues from their environment; this could be reflected in their sense organs, for instance, cocked ears and dilated pupils.

13. The human species

We close with some less formal observations. In the human family the mother is continually monitoring the state of well being of her offspring based on general activity level, changes in sense organs such as 'sparkle' in the eyes, and what goes under the broad title of 'moods'. Further clues are picked up if necessary by monitoring body temperature, sensations of pain, excretions and so on. Beginning with this ancient heritage, human societies with their complex social ties going beyond kinship level have erected a whole system of monitoring of health status through increasingly specialized professionals detecting increasingly subtle cues. Communication of well-being has indeed been tremendously elaborated in human societies.

Acknowledgement

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