International Journal of Comparative Psychology, Vol. 12, No. 4, 1999

STUDIES OF TEMPERAMENT IN SIMIAN PRIMATES WITH IMPLICATIONS FOR SOCIALLY MEDIATED LEARNING

Hilary Box
University of Reading, UK

ABSTRACT: The functions of social learning concern the acquisition of skills and information that enable individuals to adjust competently to their environments. However, individuals differ in the extents to which they cope with, maintain and create social and other environmental opportunities. Hence, it is relevant to consider dispositions of individuals interactively - as with emotion, attention and activity; to emphasise self regulatory behaviour, as with selective attention towards or away from environmental conditions. These propensities facilitate positive and negative responses that are associated with the uptake and use of skill and information from other individuals. In these regards, the study of temperament has fertile but mainly unexplored potential. Examples are given from studies of simian primates in which differences in temperament have predictive implications for social learning. When relatively fearful animals confront challenging situations, they are likely to avoid them and become physiologically disturbed. Less fearful and active animals interact more, and in emotionally more positive ways with other individuals. They are more likely to maintain closer physical proximity to others, to attend more to what they are doing and where. Hence, they have greater chances of facilitating advantageous responses - as in feeding strategies. In the acquisition of social skills, less fearful animals engage in play activities more than relatively fearful animals. Such interactions facilitate the development of information about other individuals, and the quality of social behaviour that is developed. These examples show the value of an integrative approach to behavioural studies - in which behaviour is considered with other biological systems.

The aim of this paper is to discuss interactions between two key areas in behavioural biology – with simian primates as examples. One area refers to studies of individual differences with more specific reference to the domain of temperament, the other area is that of socially mediated learning. Temperament is undoubtedly a very broad concept but it may be described generally as the characteristic style of emotional and behavioural response of an individual in a variety of different situations (Prior, 1992) that is often, but not invariably,

---

Address correspondence to Dr Hilary Box, The University of Reading, Department of Psychology, Earley Gate, Whiteknights, PO Box 238, Reading RG6 6AL, UK.

© 2000 International Society for Comparative Psychology

demonstrated very early in life. It is the stance that an individual takes towards its environment across time and situations. It refers to styles of responsiveness and not to specific acts. It involves both behavioural and other biological correlates of responsiveness to unfamiliar and challenging environmental events in all aspects of the environment - both animate and inanimate. Hence, it influences the ways in which individuals cope with everyday environmental events and the competence of their natural development.

Socially mediated learning may be described as the acquisition of information and skill (at least to some extent) from the behaviour and/or products of other individuals (Box, 1984; Heyes, 1994). Let us consider straight away why looking interactively at studies of temperament and socially mediated learning is important. Hence, the functions of social learning concern information that enables individuals to adjust competently to the demands of their environments. Moreover, developmental competence in this regard involves, for example, both physiological (as with emotional) and behavioural (as with activity and exploration) responsiveness to the challenging conditions of the social and physical environment. Behavioural and physiological measures are interactive; animals of significantly different biobehavioural dispositions react with their environments, and learn different things about those environments in different ways. In other words, individuals differ in the extents to which they cope with, maintain and create social and other environmental opportunities, and these are propensities that facilitate positive and negative responses that are associated with the acquisition and use of skill and information from other individuals. In these regards, the study of temperament has fertile but as yet mainly unexplored potential (Box, 1999). Moreover, one of many good reasons for taking examples of primates (in this way) is that there has been so much emphasis upon the potential influences of mental abilities on social learning, but relatively little upon interactions among emotional, motivational and social influences (eg Box, 1994). Importantly, studies of differences among individuals in these areas will encourage potentially new domains of understanding in social learning, and generate hypotheses for research.

Further, the primates are an interesting group with reference to studies of socially mediated learning for many reasons. For example, young primates of the two hundred and fifty or so species of living primates live in many different habitats in predominantly tropical and subtropical regions. As a group, they also eat many different kinds of foods, and although there are species that primarily select insects, fruits and flowers or foliage, and are thus relatively specialised in their diets, many species are rather loosely described as 'generalist omnivores'.

Hence, they have a good deal to learn from others about what foods to eat.

Primates are also born into a wide diversity of social organisational systems; they may live predominantly with their mothers, in family groups or in units that are made up of many individuals. Primate social systems include some of the most complex among mammals. Further, compared with most other mammals of similar body size, simian primates have large brains, long lifespans, long interbirth intervals, complex modes of parental care, and long prereproductive phases of development, as in periods of adolescent sterility (Eisenberg, 1981) that may provide opportunities for acquiring skill and information in socially mediated ways. Moreover, behavioural development among such animals continues over their lifespan, and involves the continual adjustment of individuals to the diversity of social and ecological features of their environments. In all, there is much to learn about the social complexities of the species, about gender and age, about co-operative and competitive behaviour, about mating and rearing offspring, about avoiding potential hazards such as predators and harsh weather, and about obtaining food and other maintenance behaviours. Mistakes can be very costly. Therefore it is important to consider the relative extents to which individuals cope with, and create environmental opportunities.

STUDIES OF TEMPERAMENT

The study of temperament in human behaviour has a very long history – over centuries; it has also included interest in both behavioural and other biological correlates (Rothbart, 1989). There are many well known studies with children (Kagan et al, 1992) for instance, that describe distinct and opposite clusters of measures of responsiveness that are based around approach and avoidance to challenging situations, as when children are confronted with unfamiliar surroundings and/or people.

Studies of temperament also cover a very wide range of animal groups; they include fish (eg Francis, 1990; Budaev, 1997) and octopus (Mather and Anderson, 1993). Among mammals well-known observations of individual differences in temperament within wolf litters have been associated with predatory success and social status, for example (Fox, 1972). Breeds of dogs have been extensively studied for temperamental differences among them (Scott and Fuller, 1965; Goddard and Beilharz, 1985; Willis, 1995). There has also been

selective breeding, as for emotional responsiveness, among species of rodents (eg. Gray, 1971).

Moreover, among monkeys there is a growing and substantive literature to support a sound framework within which consistent differences in behavioural and physiological responsiveness to environmental events may be described both within and among species (Clarke and Boinski, 1995). For example, rhesus monkeys have been used a good deal in this area, and with a variety of environmental challenges; they have been studied intensively in captivity singly as individuals, and in social groups. They are also increasingly studied in nature in this domain. Further, among the variety of measures that may be taken to assess temperamental responsiveness in such animals, differences in physiological responsiveness as in the hypothalamic – pituitary axis and the sympathetic nervous system are commonly used (cf. Higley and Suomi, 1989). More specifically, physiological reactivity is often measured by heart rate variability, cortisol and by central amines such as norepinephrine and serotonin. Reactive individuals physiologically, are much more likely to have significantly higher baseline levels in the turnover of catecholamines – especially norepinephrine, and to have higher, less variable heart rates than unreactive individuals. Behaviourally, individual rhesus monkeys that are reactive, are less likely to approach the unfamiliar; they have longer latencies to respond when they do approach; they are more inhibited socially and less likely to initiate social interactions with unfamiliar animals. In brief, they are more fearful and less likely to attempt all forms of challenges in their environments. It is also important for studies of socially mediated learning, for example, that significant differences in temperamental responsiveness may be identified at the time when young monkeys begin to leave their mothers and explore their environments; these differences are stable over time and situations (Suomi, 1991).

Moreover, although the majority of young monkeys within both wild and captive populations of rhesus, explore and take interest in a whole range of unfamiliar conditions, to which they also respond with minimal physiological arousal and show less intensity of behavioural responses, some 20% of the monkeys with the same background and environmental conditions, show consistent behavioural disruption and elevated physiological responsiveness. These monkeys are behaviourally withdrawn in initial interactions with their age mates; they are reluctant to leave their mothers, and explore their environments less. They show withdrawal and behavioural depression to events such as maternal separation. By contrast, individuals that are not reactive

and behaviourally inhibited begin to move away from their mothers earlier. They stay away for longer, and at greater distances; they take advantage of new inanimate situations. Further, individuals that move away from their mothers earlier are usually also those that are first to initiate interactions among their peers when they first meet them (cf. Suomi, 1997).

In addition to the 20% or so of animals that was just mentioned, there is another subgroup of monkeys that account for an additional 5 – 10% of a population that is generally described as impulsive, and particularly in the context of aggressive interactions. Critically, these individuals have low concentrations of central nervous system serotonin activity. There is a whole area of developing research here but we may just note at this point that these are individuals that are impulsive risk takers - as in play, in aggressive and locomotor behaviour; they migrate earlier than normal, are less social and lack social skills; they lack social support and seem less able to regulate their behaviour. There are clearly various implications for behavioural development. There are also increased physical risks as with injuries such as falls and fights and, unsurprisingly, there are relatively high mortality rates (cf Suomi, 1997).

IMPLICATIONS FOR STUDIES OF SOCIALLY MEDIATED LEARNING

The information given so far is intended to draw attention to aspects of differences among groups of individuals in such a species, in which biobehavioural dispositions influence responses to environmental events. It is not meant to imply specific generalizations across species but to point up the systems of responsiveness that are involved among such animals. We may now begin to consider natural contexts of behavioural development in which studies of temperament have implications for socially mediated learning and, in particular, with reference to mediating processes in social learning. For example, social attention is critical for social learning; it provides means whereby individuals may take advantage of the information that is available from other individuals, and learn to regulate their behaviour with reference to others. Very young infants are vulnerable and inexperienced, and although in some species such as marmosets and tamarins (Callitrichidae) they are cared for by members of their social groups in addition to their mothers (Yamamoto 1993), the vast majority of infant monkeys and apes are directly dependent upon their mothers for protection against environmental hazards, as well as for their

transportation and nutritional needs. The constant intimate contact in which infants are carried during all the daily activities of their caretaker(s) has important consequences in providing opportunities for socially mediated learning. For example, a young infant may view all its social and ecological environment with close reference to the responsiveness of its mother; in clinging to her ventrum it has access to information by her consistent involuntary responses to environmental events. Pereira and Altmann (1985) in discussing simian species suggest that "the infant probably also becomes sensitive to its mothers tension or calm in social and other situations and becomes conditioned to these contingencies ....." (p.231).

The world of totally dependent infants is gradually interspersed with the acquisition of more independent activities. For example, these are animals in which there is a long period of overlap when infants are both taking their mothers milk, as well as acquiring the digestive tolerance for, and selection of food, together with the skills for feeding independently. There have been pertinent observations of socially mediated feeding at this stage (Whitehead, 1986). The period before nutritional independence is also that in which infants begin to explore the environment; there are opportunities not only to gain information about foods, but about interactions with other individuals. Around eighty per cent of infant rhesus monkeys, for example, are born in a period of two to three months. Hence, each infant has many other monkeys of around the same degree of social and physical competence with which to interact. Once again, the mother is of major importance, and there is frequent emphasis upon her role in providing a secure base of emotional attachment from which an infant may explore and learn about its environment. Moreover, Boccia and Campos (1987) emphasise that in order to act as a secure base, the mother also serves as a reliable source of information about how to respond to the environment. They consider that from an infant's perspective, it is advantageous to acquire information about conditions that create uncertainty. We may refer to this process generally as "social referencing". Hence, by acquiring information, an infant, in this case, gains both knowledge about the environment, and the emotional security to act upon it. It is also an advantage to the mother to attract the attention of her infant and communicate information about environmental events – as in dangerous situations. There are experiments that are directly relevant to this issue. For example, experiments by Boccia and Campos (1987) manipulated positive and negative emotional responses of human mothers to strangers. These were found to significantly influence the responses of their offspring in

the same affective direction. The results showed that infants monitored the affective signals of their mothers and appeared to regulate their responses to a stranger both in expressive and attentional behaviour. This is important because monitoring and/or soliciting information about the social environment will influence socialization. There have been few studies on social referencing among monkeys and apes, but there are some stimulating results for further work. For instance, Evans and Tomasello (1986) found that young captive common chimpanzees (*Pan troglodytes*) discriminated the relationships of their mothers with other adult females of the social group, and adjusted their own behaviour to them accordingly.

Importantly, experiments in this domain provide useful means whereby we can study the acquisition of social information among primate species. There is so much emphasis upon the acquisition of skill such as in foraging strategies, but relatively little upon the acquisition of social information. This is an important omission for species that live in long lasting social groups with relatively complex patterns of social interaction that are central to their life strategies. For all studies of the acquisition of skill and information however, questions that refer to differences in temperamental disposition add further perspectives. As we have noted for instance, reactive and behaviourally inhibited infants interact with their mothers in ways that are different from those monkeys that are relatively unreactive and behaviourally uninhibited. Infants 'use' their mothers differently in her potential 'role' of providing a secure base in emotional security and in providing relevant information. For example, unreactive and unhibited individuals move away from their mothers earlier; they stay away longer; they also take advantage of new situations , and initiate social interactions when they first come across unfamiliar individuals. Interestingly, much may depend upon the disposition of the mother, but it is an advantage of being an outgoing – unfearful individual to develop greater behavioural flexibility in coping with environmental events; to have a wider potential network of social information in dealing with the social and physical environment. By some contrast reactive, inhibited individuals may well be animals that are at risk from other members of their social group. Hence, there are clear advantages in their reluctance to leave their mothers. They may depend upon the information that she provides as well as upon her immediate protection.

Infants cease to be infants and become juveniles when they obtain food, avoid hazards such as predators and keep up with their group – independently (Pereira and Altmann, 1985). Although they do maintain relationships with their caretakers for some time, they gradually become

independent members of their social groups. Their predominant behaviour involves exploring their environment and playing socially. Importantly, individuals are still relatively inexperienced about their physical and social environments, a situation that is compounded by the fact that they have relatively little social support. Unsurprisingly, there are still considerable risks of mortality during the early phase of the juvenile period. Hence, it is critical at this stage to acquire skills for survival that include knowledge about, and avoidance of, hazards such as predators. In later juvenilehood, developing skills, particularly the social skills that are required for success as an adolescent and as an adult, become particularly important, and are gradually developed (Pereira and Altmann, 1985).

For a physically independent but naïve animal, learning how to deal with the environment is facilitated by proximity to experienced individuals. In many situations, social attention depends upon physical proximity among individuals. For instance, Coussi-Korbel and Fragaszy (1994) emphasise that tolerance of spatial proximity supports visual observation of both the affect and activities of other individuals, together with physical access to the places and objects that are used by the other animals. When primate infants are very young they are carried by, and subsequently follow their mothers into proximity with sources of food, resting places and other animals. Gradually, infants determine independently the time that they spend in proximity and interactions with their social and physical environment. Critically then, spatial proximity involves seeking and tolerating, inter-individual distances within which information may be communicated. Hence, once again, differences among individuals in temperamental dispositions are important in creating opportunities for socially mediated learning. Individuals that are bolder and less reactive will have advantages from both seeking and tolerating physical proximity with others – they will do this more frequently, in more positive emotional responsiveness, and at an earlier time. For example, Pereira and Altmann (1985) note that apart from gaining physical protection per se, time spent by young juveniles in proximity to adults provides a context in which they may readily react to, and learn about the alarm and cautious behaviour of adults in dangerous situations. Further, because younger juveniles are permitted close proximity to older experienced animals, they are able to feed on high quality food patches and learn "to identify and process different food items" (p.240).

Discussion about activities of social play in the development of physical and social competence are familiar in behavioural biology. In socially mediated learning play provides opportunities for individuals to

gain information about other individuals as individuals, as well as about patterns of social interaction. There are significant quantitative differences among species, and with individuals of different age and gender in different ecological and social conditions. Young rhesus monkeys begin to associate mainly with their own gender in play activities from around four to five months old (Suomi, 1991). This continues throughout the second year of life. Males engage in much rough and tumble play with all monkeys that will participate. However, females stop participating in rough and tumble play from about six months old, and they rarely initiative such activities. They spend more time in grooming and chasing with other females, and competitive behaviour among them relates critically to competition for food as critical ecological constraints in their reproductive success. Furthermore, as young females grow older into adolescence, they play very little and then, mainly with young juveniles and infants. By contrast, young males continue to play well into their adolescence, predominately with their age-sex peers and thereby continue to develop their competitive skills. Further, when rhesus monkeys are about four months old their bouts of play are very short; they occur with one other animal, and with very simple behavioural sequences. Later on, at between two and three years of age, social play occupies a similar amount of time but occurs in much longer bouts, and frequently engages two or more animals. Social play is very much more complex in which coalitions among individuals are formed and reversed. Play includes elementary forms of behaviour that are used by adults to coordinate a variety of social and reproductive behaviour (Suomi, 1991). Hence, play behaviour provides information for socially mediated learning in various natural contexts. Importantly, there are good indications that differences among individuals in the extents to which they play spontaneously in later infancy, are predictive of such differences into childhood and adolescence; further, that play behaviour is inhibited by patterns of responsiveness that are more reactive and behaviourally inhibited (Higley, 1985). Moreover, young monkeys with relatively insecure attachments to their mothers play less often and show less sophisticated patterns of interactions in play than those monkeys that are securely attached (Higley, 1985). Hence, it is important generally with regard to the many opportunities for social learning that play behaviour provides, that less reactive animals engage in more play than reactive ones, and that they are more likely to initiate play activities.

The development of social skills involves a variety of dimensions of social competence that reflect the demands of complex and changing social interactions. These include competitive and co-operative

strategies; they involve co-operative alliances, reconciliation and social status. A good deal of work is needed here with reference to differences in temperament. However, there are some interesting findings with regard to social status. This is a critical area of social competence that involves priority of access to resources such as food, mates and shelter, that are necessary for survival and fitness. We may note, for example, from various studies in captivity, and in the field, that although we need more detailed information, there is an association between lack of high social status and fearful reactive responsiveness in the work with rhesus monkeys. It has been found in captivity for example (Scanlan, 1987) that reactive animals were more likely to give way, to acquiesce, to other monkeys in social interactions, or in situations where there was competition for resources. Further, that in the field, Rasmussen and Suomi (1989) found that low reactive rhesus males had profiles of behaviour that would facilitate success in competitive interactions. Further, studies of temperamental responsiveness have drawn attention to some interesting complexities. Sapolski's work (eg Sapolski and Ray, 1989; Ray and Sapolski, 1992) on free ranging savannah baboons has shown for example, that high status males include both individuals that have a high reactive style of responsiveness to environment challenge, as well as those that have a low reactive style of responsiveness. In brief, individuals who consistently showed less intense behavioural responses to psychological stressors such as capture – and were also able to distinguish between the salience of their response to different intensities of stressors (such as between the presence of another adult male compared with actually being threatened by him) also had low basal concentrations of cortisol. In contrast, dominant males who were highly reactive to identical stressors had basal cortisol levels comparable to those of subordinate adult males (Sapolski, 1990). This work is very important in showing the potential complexities of clusters of temperamental dispositions in complex behavioural interactions. It also draws attention to interrelations between endocrine activity and styles of social information processing. Moreover, higher levels of stress responsiveness among the high status males that were highly reactive to environmental challenges lowered their immune responsiveness and increased their susceptibility to health hazards as with cardiovascular disease (Sapolski, 1990).

It is obviously critical to the whole development of the area of temperament and socially mediated learning to recognise such complexities. It is also the case however, that we have a variety of information that leads to fruitful hypotheses towards the understanding

and prediction of socially mediated learning that we also need to develop. At this point we may emphasise and recapitulate some of the points that were made earlier. Hence young, unreactive and uninhibited animals as in rhesus monkeys, are more active; they move around and explore more. They also become less disturbed physiologically. In other words, they cope better especially with unfamiliar situations. Importantly, these are responses that increase the probability that less fearful individuals will confront, attend to, and become familiar with previously unfamiliar features of their environments. When relatively fearful individuals confront challenging situations, they are more likely to avoid them and become physiologically disturbed. Moreover, less fearful and active animals interact more, and in emotionally more positive ways with other animals. They are more likely to maintain closer physical proximity to others, to attend more to what others are doing and where. Hence, they may have greater chances of facilitating advantageous responses to environmental challenges – as in feeding strategies. Again, in the acquisition of social skills, less fearful animals engage in play activities more than relatively fearful animals. Such interactions facilitate the development of information about other individuals, and about the quality of a range of social behaviours that is developed. Moreover, it is important to consider that individual variations in temperamental dispositions among animal populations are robust and represent the range of individual differences that has been selected for (eg Wilson, 1998). Hence, it is also important that we should consider the advantages and disadvantages of such variations. It is interesting to consider, for example, that in large socially complex social units such as are found among many species of the simian primates, an extensive range of temperamental dispositions may allow for the exploitation of a wider range of social success, whilst at the same time reducing direct competition among individuals (Clark, 1991).

Differences in temperamental dispositions among species of monkeys also raise functional questions with regard to socially mediated learning. There is not a large number of studies but there are some interesting hypotheses. Species have been studied with a variety of unfamiliar social and inanimate challenges. Moreover, there are robust data to support hypotheses that associate interrelationships among species typical temperamental responses with their social and ecological systems (Clarke and Boinski, 1995). As with the findings for individuals within species, the shy-bold/reactive-unreactive dimensions of comparison are apparently the most appropriate (Clarke and Boinski, 1995).

Tentative hypotheses for such differences include defence against

predation, feeding and habitat specialisations. Clarke and Boinski (loc cit) note for example, the hypothesis that species that are more curious, bold, unfearful and instrumental in their approach to unfamiliar situations are also those that utilise relatively high energy foraging strategies and/or complex foraging, and tend to have 'omnivorous' diets. Given the emphasis that has been placed upon rhesus monkeys in this paper, it is interesting to consider comparisons among species of the same genus (*Macaca*). Moreover, the macaques are potentially a good model for such comparisons. Hence, the twenty or so species live in many different habitats across Asia; they eat many different foods (Melnick and Pearl, 1987); there are also differences in ranging behaviour, habitat use and foraging behaviour, and there are differences in sexual and social behaviour (cf. Clarke and Boinski, 1995). Interestingly, there is now good evidence on the basis of a variety of social and inanimate challenges, that a number of species are behaviourally and physiologically distinct (eg. Clarke and Mason, 1988; Clarke *et al.*, 1988; Clarke and Lindburg, 1993; de Waal, 1989; Thierry, 1985). Responsiveness varies greatly in different challenging situations. There are significant interspecific variations, for example, in aggressiveness, in reconciliatory behaviour, in curiosity and exploratory behaviour. Hence, among a number of species of the macaques, rhesus monkeys are bold and unreactive in their approach to unfamiliar environmental events. They are relatively exploratory; they are the most aggressive and the least conciliatory; they are less passive socially. Interestingly, this is a species that is very widely distributed, and thrives in a diversity of ecological conditions . It is interesting to consider for instance, that individuals that are relatively reactive, and inhibited, may be comparatively disadvantaged in such a species.

Comparative studies among the macaques also serve to highlight the influence of 'social support' in behavioural development namely, the amount of affiliative behaviour directed towards an individual (Boccia *et al.*, 1997). Bonnet macaques (*M. radiata*), for example, have a different social developmental network than pigtail macaques (*M. nemistrina*) with which they are often compared. Bonnet monkeys have a relatively open social system; mothers are less restrictive and infants interact freely and frequently with numbers of group members. Social attachments are formed with more individuals than among young pigtail monkeys. There are immediate implications for social learning. Differences in social networks are important for routes of transmission of behaviour, as in social attention to a wider social nexus, that also provides information about the environment in affiliative contexts. Moreover, individuals of these two species respond differently -

physiologically and behaviourally to environmental challenges. Importantly,the natural availability of alternative social attachments can modulate against the physiological and behavioural consequences of aversive events. Further, infant bonnet monkeys without such social support are not buffered against adverse environmental events. The critical point is that the different social organisational style of bonnet monkeys provides the opportunity to ameliorate expressions of negative responsiveness,and provides increased opportunities for socially mediated learning of positive responsiveness to environmental events. Social support both modulates physiological responsiveness and facilitates social attachment, which in turn may facilitate security, exploration and exposure to information that is available from other group members. We might also note that social opportunities of social support not only influence the ability of individuals to cope with their environments, but to remain healthy and reproductively fit. Hence, there are also issues that are relevant to health, welfare and conservation in both natural and captive conditions. For example, developing research in the field of psychoneuroimmunology is of interest in this context (eg Laudenslager and Boccia, 1996).

In conclusion, the examples given in this paper draw attention to differences in biobehavioural dispositions that influence learning in a variety of contexts. The fact that they have not been considered with reference to familiar discussions of animal social learning is an omission in our thinking in this area.

The point is that the interrelationships among biobehavioural propensities within individuals of different species have implications for their opportunities to acquire and use skill and information from other animals. Hence, interactive studies among such biobehavioural propensities represent realistic approaches of study in this area, and emphasise that such learning is socially mediated.

ACKNOWLEDGEMENTS

I thank Gisela Kaplan warmly for her invitation to attend the symposium in Bangalore . I also thank one anonymous reviewer and both Lesley Rogers and Gisela Kaplan for their helpful comments on the manuscript. This contribution is based upon a chapter by the author that appeared in Box, H.O. and Gibson, K.R. (Eds) *Mammalian Social Learning: comparative and ecological perspectives*. Cambridge University Press 1999.

REFERENCES

Boccia, M.L. & Campos, J.J. (1987) Social attentional processes in human and non-human primate infants. *Primate Report*, *18*, 3-10.

Boccia, M.L., Scanlan, J.M., Laudenslager, M.L., Broussard, C.L. & Reite, M.L. (1997) Presence of "friends" mitigates behavioral and immunological responses to maternal separation in bonnet macaques. *Physiology and Behavior*, *Vol 61*, 191-198.

Box, H.O. (1984) *Primate Behaviour and Social Ecology*, Chapman and Hall, London.

Box, H.O. (1999) Temperament and socially mediated learning among primates. In H.O. Box and K.R. Gibson (Eds.), *Mammalian Social Learning: comparative and ecological perspectives* (pp. 33-56). Cambridge University Press.

Box, H.O. (1994) Comparative perspectives in primate social learning: New lessons for old traditions. In J.J. Roeder, B. Thierry, J.R. Anderson and N. Herrenschmidt (Eds.), *Current Primatology (*pp. 321-327). Universite Louis Pasteur, Strasbourg.

Budaev, S.V. (1977) "Personality" in the guppy *(Poecilia reticulata)*: a correlational study of exploratory behavioural and social tendency. *Journal of Comparative Psychology*, *111*, 399-411.

Clark, A.B. (1991) Individual variation in response to environmental change. In H.O. Box (Ed.), *Primate Responses to Environmental Change* (pp. 91-110). Chapman and Hall, London.

Clarke, A.S. & Boinski, S. (1995) Temperament in Nonhuman Primates. *American Journal of Primatology*, *37,* 103-125.

Clarke, A.S. & Lindburg, D.G. (1993) Behavioural contrasts between male cynomologous and lion-tailed macaques. *American Journal of Primatology*, *29*, 49-59.

Clarke, A.S. & Mason, W.A. (1988) Differences among three macaque species in responsiveness to an observer. *International Journal of Primatology*, *9*, 347-364.

Clarke, A.S., Mason, W.A. & Moberg, G.P. (1988) Differential behavioural and adrenocortical responses to stress among three Macaque species. *American Journal of Primatology*, *14*, 37-52.

Coussi-Korbel, S. & Fragaszy, D.M. (1995) On the relation between social dynamics and social learning. *Animal Behaviour*, *50,* 1441-1453.

de Waal, F.B.M. (1989) *Peacemaking Among Primates*. Harvard University Press, Cambridge, M.A.

Eisenberg, J.F. (1981) *The Mammalian Radiations*. University of Chicago Press, Chicago.

Evans, A. & Tomasello, M. (1986) Evidence for social referencing in young chimpanzees (*Pan troglodytes*). *Folia Primatology*, *47*, 49-54.

Fox, M.W. (1972) Socio-ecological implications of individual differences in wolf litters: a developmental and evolutionary perspective. *Behaviour*, *41*, 298-313.

Francis, R.C. (1990) Temperament in a fish: A longitudinal study of the development of individual differences in aggression and social rank in the Midas Cichlid. *Ethology*, *86,* 265-352.

Goddard, M.E. & Beilharz, R.G. (1985) A multivariate analysis of the genetics of fearfulness in potential guide dogs. *Behaviour Genetics*, *15*, 69-89.

Gray, J.A. (1971) *The Psychology of fear and stress*. McGaw Hill, Toronto, N.Y.

Heyes, C.M. (1994) Social learning in animals: Categories and mechanisms. *Biological Reviews*, *69*, 207-231.

Higley, J.D. (1985) Continuity of social separation behaviours in rhesus monkeys from infancy to adolescence. Unpublished doctoral dissertation, University of

Wisconsin, Madison, WI.

Higley, J.D. & Suomi, S.J. (1989) Temperamental Reactivity in Non-Human Primates. In G.A. Kohnstamm, J.E. Bates and M.K. Rothbart (Eds.), *Temperament in Childhood* (pp. 153-167). John Wiley and Sons Ltd.

Kagan, J., Snidman, N. & Arcus, D.M. (1992) Initial reactions to unfamiliarity. *Current Directions in Psychological Science, 1,* 171-174.

Laudenslager, M.L. & Boccia, M.L. (1996) Some observations of Psychosocial Stressors, Immunity, and Individual Differences in Nonhuman Primates. *American Journal of Primatology, 39*, 205-221.

Mather, J.A. & Anderson, R.C. (1993) Personalities of octopuses (*Octopus rebescens*). *Journal of Comparative Psychology, 107*, 336-340.

Melnick, D.J. & Pearl, M.C. (1987) Cercopithecines in multimale-groups: Genetic diversity and population structure. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker (Eds.), *Primate Societies* (pp. 121-134). University of Chicago Press, Chicago.

Pereira, M.E. & Altmann, J. (1985) Development of social behaviour in free-living nonhuman primates. In E.S. Watts (Ed.), *Nonhuman Primate Models for Human Growth and Development* (pp. 217-309). Liss New York.

Prior, M. (1992) Childhood Temperament. *Journal of Child Psychiatry, 33*, 249-279.

Rasmussen, K.L.R. & Suomi, S.J. (1989) Heart rate and endocrine responses to stress in adolescent male rhesus monkeys on Cayo Santiago. *Puerto Rico Health Science Journal, 8*, 65-71.

Ray, J.C. & Sapolski, R.M. (1992) Styles of male social behaviour and their endocrine correlates among high ranking baboons. *American Journal of Primatology, 28*, 231-50.

Rothbart, M.K. (1989) Biological Processes in Temperament. In G.A. Kohnstamm, J.E. Bates and M.K. Rothbart (Eds.), *Temperament in Childhood* (pp. 77-110). John Wiley and Sons Ltd.

Sapolski, R.M. (1990) Adrenocortical function, social rank, and personality among wild baboons. *Biological Psychiatry, 28*, 862-878.

Sapolski, R.M. & Ray, J.C. (1989) Styles of dominance and their endocrine correlates among wild olive baboons (*papio anubis*). *American Journal of Primatology, 18*, 1-13.

Scanlan, J.M. (1987) Social dominance as a predictor of behavioural and pituitary-adrenal response to social separation in rhesus monkey infants. Paper presented at the meeting of the *Society for Research in Child Development*. Baltimore, MD, April 1987.

Scott, J.P. & Fuller, J.L. (1965) *Dog Behaviour: The Genetic Basis*. University of Chicago Press, Chicago and London.

Suomi, S.J. (1985) Biological response styles: experiential effects. In H. Klas and L.J. Siever (Eds.), *Biologic Response Styles: Clinical Implications* (pp. 2-17). American Psychiatric Press, Washington, DC.

Suomi, S.J. (1991) Uptight and laidback monkeys. In S.E. Brauth, W.S. Hall & R.J. Dooling (Eds.), *Plasticity of Development* (pp. 27-56). MIT Press Cambridge, M.A.

Suomi, S.J. (1997) Early determinants of behaviour: evidence from primate studies. *British Medical Bulletin, 53,* 170-184.

Suomi, S.J., Rasmussen, K.L.R., & Higley, J.D. (1992) Primate models of behavioural and physiological change in adolescents. In E.R. McAnarney, R.E. Kreipe, D.P. Orr & G.D. Comerci (Eds.), *Textbook of Adolescent Medicine* (pp. 135-139). Philadelphia: Saunders.

Thierry, B. (1985) Patterns of agonistic interactions in three species of macaques (*macaca mulatta, M. fascicularis, M. tonkeana*). *Aggressive Behaviour*, *11*, 223-233.

Whitehead, J.M. (1986) Development of feeding electivity in mantled howling monkeys *Alouatta palliata*. In: J.G. Else & P.C. Lee (Eds.), *Primate ontogeny, cognition and social behaviour* (pp.105-117). Cambridge University Press.

Willis, M.B. (1995) Genetic aspects of dog behaviour with particular reference to working ability. In J. Serpell (Ed.), *The Domestic Dog: its evolution, behaviour and interactions with people* (pp. 54-64). Cambridge University Press.

Wilson, D.S. (1998) Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London*, *Series B353*, 199-205.

Yamamoto, , M.E. (1993) From dependence to sexual maturity: the behavioural ontogeny of Callitrichidae. In: A.B. Rylands (Ed.), *Marmosets and Tamarins: Systematics, Behaviour and Ecology* (pp.235-254). Oxford University Press.