

## 4 Individuality in the domestic cat: origins, development and stability

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## Introduction

Dolly was a long-haired silver tabby with the supercilious mannerisms of a pure-breed. Tivvy was short-haired, his coat greyish brown, his disposition most affectionate: he would jump on your lap if you sat reading, get between your face and your book, and, talking and purring prodigiously, pat your cheek with a curled paw until you agreed to stop reading and pet him. Nicky, whose short black fur was tinged with red, was a problem child from the start. He was the scariest, took the longest to tame, bitterly resented correction of any kind.

*Wilson & Weston (1947).*

The phenomenon of individuality or personality in domestic cats is familiar to most cat owners. Anyone who owns a pet cat and spends time observing and interacting with it is likely to develop a strong impression of that animal's behavioural characteristics. From this knowledge of the cat's behaviour, the owner may go on to view the animal as an individual with a distinct character, similar to other cats in certain respects, but different in others. That many cat owners do indeed perceive their pet cat as a unique individual is reflected in the popular literature on the domestic cat in which references to individuality and personality abound (e.g. Chazeau, 1965; Necker, 1970; Rockwell, 1978; Johnson & Galin, 1979; Metcalfe, 1980; Alderton, 1983; Palmer, 1983).

In an earlier review (Mendl & Harcourt, 1988) we attempted to make a start at defining what is meant by individuality in the domestic cat, and at possible ways of approaching the scientific study of this phenomenon. Since that time, there has been an increased interest in the existence of individual distinctiveness in animals in general. In this chapter, we review some of the advances that have been made in studies of the domestic cat. As before, we begin by examining how individuality can be measured, and the sorts of questions that can be asked about it. The main part of the chapter then focuses on topics which have received most attention recently; the origins and development of individuality in cats, and its stability across time and context.

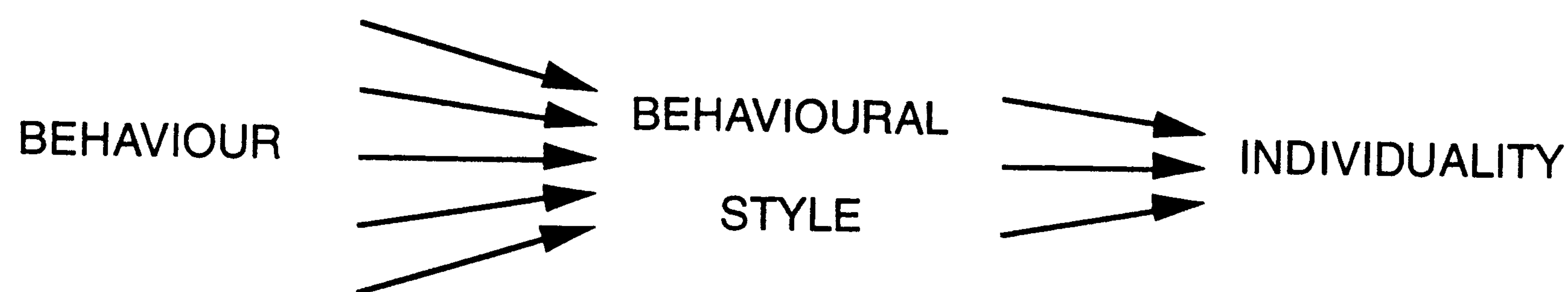
### What is meant by individuality?

The terms individuality, personality and temperament are often used interchangeably in studies of animals (Lyons, Price & Moberg, 1988; Loughry & Lazari, 1994; Fagen & Fagen, 1996). In general, they

are used as descriptive labels for the complex mental pictures which people have of individual animals. One way of describing these mental images is as a perception of the sum total of all the behavioural attributes which characterise the individual and which distinguish it from others of the same species. For example, Feaver, Mendl & Bateson (1986) stated, 'We felt that each animal (cat) in our laboratory colony had a distinct personality in the sense that the sum total of its behaviour gave it an identifiable style.'

How do we arrive at this concept of the 'sum total' of an animal's behaviour? Consider an observer watching several cats. Through time he or she may interact with the animals and watch them behave in a variety of situations. Differences in how particular individuals perform specific behavioural actions and in how they interact with one another may become evident. Through observation of these differences, the observer gains an impression of the general patterning and nature of each animal's behaviour in relation to that of others. The general features that distinguish the behaviour of the individuals can be given names. For example, adjectives such as 'friendly', 'curious', 'nervous', 'bold' may be used to refer to the overall patterns of each animal's behaviour which remain elusive when discrete events are considered on their own. These characteristics are called aspects of behavioural style (see Feaver *et al.*, 1986). Finally, the various behavioural styles perceived to be typical of a particular cat are assimilated in the mind of the observer to achieve an overall perception of that animal's individuality. Thus individuality of a cat is the result of a mental abstraction from direct observations of the animal's behaviour in relation to that of others. This complex mental process is represented in a very simplified form in Figure 4.1.

As we move from individual differences in behaviour patterns to individuality (from left to right in Figure 4.1), the role that the observer plays in describing the cat's behaviour becomes increasingly complex. Perception of the individuality of a particular cat may vary between observers according to the nature of their interactions with the animal, their knowledge of other animals (with which they can compare the cat in question), the weight they give to particular aspects of behaviour and behavioural style, and so on. On the other hand, description of individual differences in a specifically defined behaviour pattern is likely to be achieved with reasonable agreement amongst observers (Caro *et al.*, 1979). This difference is reflect-



**Figure 4.1.** A simplified representation of the levels of perception of individuality. Through observation of many discrete events (left hand side), the observer may come to view the cat as having certain aspects of behavioural style (centre). The cat's various behavioural styles contribute to the overall perception of its individuality (right hand side).

ed in the fact that scientifically rigorous methods have been developed to rate, describe and distinguish individuals according to the way they perform specific behavioural acts and also in terms of aspects of their behavioural style, but not in terms of their overall individuality (Stevenson-Hinde, Stillwell-Barnes & Zunz, 1980a; Feaver *et al.*, 1986; Fagen & Fagen, 1996). Throughout this chapter we will, therefore, need to draw on examples of both individual differences in behaviour patterns and aspects of behavioural style to examine the phenomenon of individuality. The former are more common because relatively few studies have attempted to directly assess behavioural style in cats. Nevertheless, these single behaviour patterns obviously contribute to our perception of behavioural style. For example, the time taken for cats to investigate a novel object in a test situation is likely to reflect their 'boldness' or 'curiosity'.

### How can we measure individuality in the cat?

Since we wrote our original paper on individuality in the cat (Mendl & Harcourt, 1988), there have been several studies of individual distinctiveness in a range of species. The measurement of temperament and/or individual distinctiveness in cats (e.g. McCune, 1995; Turner, 1999), other domestic mammals such as pigs (Hessing *et al.*, 1993; Erhard & Mendl, 1997) and goats (Lyons *et al.*, 1988), and wild mammals such as prairie dogs (Loughry & Lazari, 1994) and bears (Fagen & Fagen, 1996), has used and developed methods which stem, in part, from earlier studies of individuality in non-human primates (e.g. Buirski, Plutchik & Kellerman, 1978; Stevenson-Hinde & Zunz, 1978; Stevenson-Hinde *et al.*, 1980a, b; Stevenson-Hinde, 1983, 1986). We briefly outline these methods here.

### Recording of behaviour in a free situation

The recording of behaviour in a free, uncontrolled situation provides a useful way of distinguishing between individuals in terms of the frequencies, durations and patterning of their behaviour. This method is scientifically rigorous since the reliability of measurement can be established (e.g. Caro *et al.*, 1979). However, although it is useful in measuring individual differences in particular behaviour patterns, it is unable to provide direct measurement of differences in more general features of behavioural style (e.g. 'nervousness', 'excitability'). Moreover, the uncontrolled nature of the situation means that there is no easy way to assess the effects of changing context on individual behaviour. In addition, to determine cross-time consistency of individuality, several recordings must be performed and it is possible that the meaning of a particular behavioural item may change with age or even seasonally (Stevenson-Hinde, 1983; Hayes & Jenkins, 1997). Despite these difficulties, measures of animals as they behave in their home situation are valuable because consistent differences between individuals are unlikely to be the result of an artificial test situation. This method has been used successfully in cats. For example, Baerends-van Roon & Baerends (1979) recorded individual differences in the development of predatory behaviour during the second and third months of kitten life, and Lawrence (1981) described individual variation in maternal behaviour.

### Recording behaviour in a structured test situation

The use of a structured test situation introduces some control into the context in which behaviour recordings are being made. Specific measures, such as latency to approach a strange person, may be recorded under standardised conditions. However, when particular test situations are implemented, it is often difficult to

know which sorts of measures (e.g. latency, duration, frequency) should be recorded (Spencer-Booth & Hinde, 1969) and how to interpret performance in terms of individual differences in other, less constrained, situations (Mendl, 1986; Erhard & Mendl, 1997). Generalisation of performance to another test or a free situation may be low (e.g. Stevenson-Hinde *et al.*, 1980a) and the degree to which tests assist in the understanding of overall individuality is limited. Nevertheless, tests may successfully demonstrate consistent individual differences in specific behaviour patterns (Armitage, 1986a; Lyons *et al.*, 1988; Erhard & Mendl, 1997). Meier & Turner (1985) and Mertens & Turner (1988) used structured test procedures to demonstrate individual differences in the responses of cats to people. Structured test situations have also been used to determine consistent individual differences over time in dominance and competitive ability of adult cats (e.g. Baron, Stewart & Warren, 1957; Cole & Shafer, 1966).

### Observer rating

This method allows two or more observers who know the animals well to provide independent ratings of each individual on a series of behaviourally defined categories such as 'equable', 'excitable', or 'flamboyant' (see Stevenson-Hinde & Zunz, 1978; Feaver *et al.*, 1986; Fagen & Fagen, 1996). These categories cannot be easily measured using conventional ethological recording techniques. Using these ratings allows observers to record subtle, higher-level aspects of the individual animal's behaviour: behavioural style, rather than merely behavioural events. The reliability of such ratings can be statistically determined by calculating the correlations between observers' ratings and by comparison with direct recording methods that focus on behaviour patterns related to these categories (Feaver *et al.*, 1986).

The value of this method lies not only in its ability to get at subtle features of an individual's behavioural style, but also through the role that the observer plays as an active instrument, filtering, accumulating and integrating information over a period of time (Block, 1977; Stevenson-Hinde, 1983; Feaver *et al.*, 1986). Although caution is required because the observer introduces a personal bias into their ratings (see Stevenson-Hinde & Zunz, 1978) it also means that rare but important events, which may pass unnoticed using conventional techniques, are given appropriate

weight in the ratings (Stevenson-Hinde, 1983). However, to use this method effectively, two or more observers require detailed knowledge of their subjects (usually over several weeks or months) and this may result in limits to the applicability of the technique. Feaver *et al.* (1986) demonstrated the reliability and validity of using the observer rating technique to measure individual differences in certain characteristics in the cat (the categories used are displayed in Table 4.1).

### Owner Report

The fine detail and clarity of authors' writings about their pet cats in the popular literature (e.g. Wilson & Weston, 1947; Chazeau, 1965) is an indication of the understanding and perception that cat owners show about their pets. Owners' reports can be harnessed through the use of interviews, free-written reports and questionnaires. These reports can then provide a useful source of information for behaviour ranging from individual eccentricities and quirks to global descriptions of aspects of behavioural style and overall individuality. Within the realm of psychology, self-report questionnaires are widely and reliably used for assessment of individual characteristics (Shrout & Fiske, 1995). Caution must, however, always be used in the interpretation of owners' reports. Descriptions of behavioural style and individuality may be affected by a variety of factors, not least the personality of the owner and their experience of and relationship with their cat. Nevertheless, in combination with more rigorous methods, owners' reports can add an extra dimension to the description of individuality. For example, Meier & Turner (1985) used interviews with cat owners to provide additional

Table 4.1. *A list of cat behavioural characteristics used in the observer rating method of Feaver et al. (1986)*

Active	Hostile to people
Aggressive	Playful
Agile	Sociable with cats
Curious	Sociable with people
Equable with cats	Solitary
Excitable	Tense
Fearful of cats	Vocal
Fearful of people	Voracious
Hostile to cats	Watchful

evidence for their classification of the owners' pets into one of two personality types and Turner (1999) extended this to ratings of the behavioural style of different breeds.

### Relating different types of measurement of individuality

All four methods of measurement outlined have their advantages and disadvantages. The first two are easy to use but only provide information about individuality at the level of simple measures of behaviour. The second two are more difficult to use in a rigorous way (especially Owner Reports) but potentially provide information about more complex behavioural characteristics or behavioural style. Behavioural style, as is clear from Figure 4.1, is more closely related to overall individuality than are simpler measures of individual differences in particular behaviour patterns. Nevertheless, it is possible to describe measures of particular behaviour patterns in terms of aspects of behavioural style. For example, Meier & Turner (1985) took standard measures of the responses of cats to a strange person and then used specified criteria to divide their sample up into individuals whose behaviour could be classified as 'trusting' or 'shy'. This approach of categorising individuals according to their behaviour scores is described by Simpson (1985).

In studies in which a number of different measurements of individual behaviour have been made, researchers have used statistical techniques to cluster together those measures which are correlated and separate those which are uncorrelated. The clusters are thought of as basic dimensions of personality or individuality. For example, Feaver *et al.* (1986) identified three uncorrelated clusters of characteristics which they termed 'alert', 'sociable' and 'equable' (Table 4.2). The scores of each individual cat on the behavioural items within each cluster were calculated to give a personality score for each cat. These sorts of method have been used in a number of studies of animal individuality (e.g. rats: Denenberg, 1970; monkeys: Stevenson-Hinde & Zunz, 1978; marmots: Armitage, 1986a; goats: Lyons *et al.*, 1988; prairie dogs: Loughry & Lazari, 1994; bears: Fagen & Fagen, 1996). However, as Stevenson-Hinde & Zunz (1978) point out, it must be remembered that the clusters produced by these methods are entirely dependent on the behaviour patterns which are selected to be

Table 4.2. *Three uncorrelated groups of cats' behavioural characteristics identified by Feaver et al. (1986)*

Group label	Component characteristics
Alert	Active, Curious
Sociable	Sociable with people, Fearful of people, Hostile to people, Tense
Equable	Equable

measured. Addition of new behavioural items or rating categories may alter the composition of the emergent groups of measures.

We have shown that measures of simple individual differences in behaviour patterns and measures of behavioural style can be related to each other, thus allowing bridges to be formed between the different levels depicted in Figure 4.1, and individuality to be studied at various levels of description. Measurement is an essential first step in answering questions about individuality. In the rest of this chapter, we consider the questions that can be asked about cat individuality, and what is known.

### What questions can be asked about individuality in the cat?

At least three major questions can be asked about the phenomenon of individuality or personality. One involves examining the proximate causes of individual variation. For example, can individual variation be directly related to variation in genetic and environmental factors? How do individual characteristics develop and change across time? Are individual differences in behaviour purely a result of differing responses to the immediate environment or are individuals consistently different in a variety of contexts? These are some of the fundamental questions that are asked about human personality and temperament (Pervin, 1980; Goldsmith *et al.*, 1987). Much of the work that has been done on individuality in the domestic cat addresses these sorts of question. Consequently, they will form the main focus of the rest of this chapter.

A second question, favoured by evolutionary biologists (Davies, 1982; Dunbar, 1982; Armitage, 1986b), focuses on the consequences of behaving in different ways. How do the particular individual characteristics of an animal affect its ability to survive and reproduce? There has been less study of this

question in the domestic cat, perhaps because such study is best carried out in non-domesticated species, and is greatly facilitated if the behaviour under consideration is expressed as a limited number of 'alternative strategies' in the population (see Mendl & Deag, 1995). At present, there is little evidence that individual differences in aspects of behavioural style in the cat can be easily categorised in this way. In addition, the problems of measuring fitness costs and benefits are substantial (Davies, 1982). Consequently, we will not examine this question in detail here (see Mendl & Harcourt, 1988, for a previous discussion of this issue), reporting only some recent work in which the link between coat colour and certain behavioural characteristics may allow us to make inferences about the reproductive success of different behavioural styles (Pontier, Rioux & Heizmann, 1995).

The third general question relates to the construction of individuality. Are there fundamental dimensions or types of personality which are characteristic of a particular species or, more interestingly, which appear to occur across species? A growing number of researchers of human personality suggest that most behavioural traits can be clustered into five broad domains known as 'The Big Five' personality factors: Extraversion, Agreeableness, Conscientiousness, Neuroticism, Openness to Experience (e.g. Goldberg, 1992; Hampson, 1995). Similarly, and perhaps more relevant to studies of animals, child psychologists have identified a limited number of basic elements of child temperament. In particular, the elements emotionality, sociability and activity (Buss & Plomin, 1986; but see Goldsmith *et al.*, 1987 for alternative views) have been likened to those observed in animal studies, such as activity, reactivity and avoidance in octopuses (Mather & Anderson, 1993) and confident, excitable and sociable in rhesus monkeys (Stevenson-Hinde *et al.*, 1980a). Recently, there has also been interest in so-called active and passive coping strategies, clusters of behaviour shown in response to challenging situations, and the extent to which these are found as distinct response styles within a species (e.g. Benus *et al.*, 1991; Hessing *et al.*, 1993; Jensen, 1995; Mendl & Deag, 1995; Erhard & Mendl, 1997). The dimensions of behavioural style detected in the domestic cat will become evident throughout the rest of this chapter.

## The origins of individuality in the cat

One obvious question that can be asked about individuality is how variation in genetic and environmental factors contributes to variation in individual behaviour (Plomin, DeFries & McClearn, 1980; Plomin, 1981). This issue has recently begun to be investigated in the domestic cat.

### Breed differences

Indirect evidence that genetic factors may exert some influence over behaviour which contributes to individuality in the cat comes from reports of behavioural differences between various cat breeds. For example, in popular books the Siamese cat is referred to as demanding considerable affection, liking attention, and talkative while the Russian Blue is described as quiet and gentle (Beadle, 1977; Johnson & Galin, 1979; Pond & Raleigh, 1979; Loxton, 1981, 1983; Alderton, 1983; Palmer, 1983).

Hart & Hart (1984) built on these anecdotal reports by surveying cat show judges who reported remarkably similar and distinctive breed characteristics. Siamese cats, for example, were reported to be the most outgoing with strangers and the most demanding of attention, with vocalisations often described as similar to talking. On the other hand, the Russian Blue was generally reported to be shy and withdrawn. A variety of other breeds were described in this way, most in agreement with the popular literature.

Fogle (1991) expanded this approach by surveying veterinarians who come into contact with many different breeds, in contrast to cat show judges whose experience may be limited to just a few. A questionnaire asked them to rank six different breeds on ten statements about behaviour such as 'are very active', 'tolerate handling well' and 'are destructive', by inserting 'always', 'frequently', 'sometimes' or 'never' by each characteristic. The common view of the Siamese as a particularly active and vocal breed was supported, and various other breed differences emerged. For example, Persians were ranked as least active and destructive, while Oriental Shorthairs and Siamese were generally ranked as the most excitable and destructive.

In a more recent questionnaire study, Bradshaw, Neville & Sawyer (1997) emphasised the breed specificity of pica behaviour, the ingestion of non-nutritive items. Turner (1999) went one step further

by combining a questionnaire study of owners' perceptions of their cats with an observational study of what owners and their cats actually did together in the home situation. He compared Siamese, Persian and 'house cats' (i.e. non-purebred domestic mixtures). Subjective ratings of the breeds by their owners indicated that both the Persian and Siamese were viewed as being different to house cats in several ways; more vocal, affectionate towards the owner and friendly towards strangers. The Siamese were also more playful, active and curious and the Persians were cleaner. There were fewer differences between the two purebreeds, the Siamese being rated as more playful and active. The direct behavioural observations of owner–cat interactions by Turner also detected breed differences. For example, purebred cats and their owners spent more time in close proximity to each other and had longer interactions than house cats and their owners. Owners of Siamese cats played with and petted their cats more than owners of the other breeds. Most interestingly, there were suggestions from a subset of data focusing on women owners in this and another study (Turner, 1991), that Siamese cats directed more vocalisations to their owners and were responsible for initiating relatively more interactions than either Persians or house cats. This again supports the view of the Siamese as a demanding and vocal breed. Clearly, cat–owner interactions are two-way processes and it is possible that some of the breed differences reported in this study could be attributable to the characteristics and expectations of owners of different breeds rather than the cats themselves. Nevertheless, observational studies of the sort carried out by Turner provide a first step towards objective behavioural measurement of differences between breeds.

Given that cat breeds are genetically distinct at certain loci, the reported differences in aspects of their behavioural style indicate that genetic factors may underlie some of the observed individual variation in behaviour. However, the existence of breed differences in behaviour tells us nothing about the mechanisms by which genes exert an influence on behaviour in the cat.

### Coat colour genetics and behavioural characteristics

Another line of evidence linking variation in behaviour to genetic variation comes from observations of

behavioural differences between cats with different coat colourings. For example, on the basis of surveys of the distribution of cats of different colouring, Todd (1977) suggested that cats carrying the non-agouti allele, usually black cats, may be more tolerant of crowding and the conditions of urban life than those carrying the agouti allele. More recently, Ledger & O'Farrell (1996) reported that in a study of 84 British Shorthair kittens, those individuals with a red, cream or tortoiseshell coat colour struggled for a longer time and made more escape attempts when handled by an unfamiliar person than kittens with other coat colours.

Pontier *et al.* (1995) extended this line of thinking by linking coat colour polymorphisms and their underlying genetic profiles, to behavioural differences and their subsequent impact upon social structure. They suggested that the orange allele may be linked to aggressiveness in males, whilst, as mentioned above, some other mutations such as the non-agouti are linked to greater amicability and aggregative tendencies (Robinson, 1977). Pontier *et al.* then used this behavioural difference to explain why the orange allele tends to be found at relatively low frequencies, at least in urban environments, compared with other, more recent mutations such as the non-agouti and the blotched tabby. In a series of papers on mating systems in cats, Natoli and co-workers demonstrated that in urban environments, where cat densities can be extremely high, aggressiveness is not related to reproductive success of males as a result of the promiscuous mating system (Natoli, 1990; Natoli & De Vito, 1991). Rather, aggressive males may actually lose mating opportunities because of their intolerance for other male cats and because they spend their time fighting rather than mating. In contrast, successful males may be seen sitting patiently waiting for their opportunity to mate a female in oestrous, and sperm competition rather than outright physical combativeness seems to be the principal mechanism in male mating success (Natoli & De Vito, 1991). Hence aggressive males with the orange allele will on average have a relatively low degree of mating success. Pontier *et al.* (1995) suggest that this explains why, despite being one of the most ancient coat-colour mutations, the orange allele has a frequency of mean 0.20 (range 0.00–0.46). This compares with a mean frequency of 0.70 (range 0.40–0.87) for the more recent non-agouti allele, and 0.40 (range 0.00–0.87) for the blotched tabby allele (Lloyd & Todd, 1989).

Further support for their hypothesis comes from comparing rural and urban cat populations. In contrast to urban environments, rural cat populations tend to be at lower densities, with animals more widely dispersed. In this environment dominant males can monopolise females more effectively, and aggressiveness may therefore be favoured (Liberg & Sandell, 1988). Rather than a promiscuous mating system, a relatively high degree of polygyny appears to operate in rural areas (Liberg, 1983; Liberg & Sandell, 1988). In concordance with this hypothesis, Pontier *et al.* (1995) show that the frequency of the orange allele is consistently greater in rural environments, suggesting that in certain circumstances, genetically linked behavioural traits may be favoured.

Relationships between coat colouring and behaviour appear to occur in a variety of other species, and a number of possible reasons for their occurrence have been suggested (Hemmer, 1990, chap. 8). First, changes in pigmentation may directly influence the function of sensory organs. For example, the lack of protective pigment in the iris of albino animals leads to problems of visual perception, especially in bright light, which may underlie some of their commonly observed behavioural characteristics, such as sluggishness of reactions.

A second possibility directly links the mechanisms underlying coat colouring to those underlying the control of behaviour. Coat colouring pigments (melanins) are produced by the same biochemical pathways as the catecholamines, such as dopamine, which play an important role in brain activity. For example, dihydroxyphenylalanine (dopa) forms the basis for the synthesis of both types of compound. It is therefore possible that there is a relationship between the supply and use of dopa in the nervous system and in the skin (Todd, 1977; Hemmer, 1990, chap. 8). If coat colouring genes help to regulate dopa usage in both systems, this might underlie apparent links between behaviour and coat colour.

A third possibility is that genes controlling coat colouring are located at positions on chromosomes close to other genes which have some influence on the function of the nervous system. For example, blue-eyed white cats and, to a lesser extent, white cats with orange eyes are often deaf. This genetically induced defect obviously has a marked effect on behaviour and caused breeders to regard these animals as 'dull of intellect and slow in thinking' (Pond & Raleigh, 1979, p. 183). It appears that the gene involved in the

production of the white coat colour may be positioned close to a gene which induces deafness in one or both ears (Hemmer, 1990), and therefore that cats inheriting one trait are also likely to inherit the other.

So, there are at least three ways in which a cat's coat colouring may be linked to its behavioural characteristics, each demonstrating a different route by which behaviour may be influenced by the actions of genes.

### Environmental variation and individuality

A number of studies have demonstrated that a kitten's early environment can have a strong influence on its behaviour later in life. Several of these studies are described in Chapter 2. We will concentrate here on behaviour patterns which can be related in a relatively straightforward way to aspects of behavioural style or individuality.

Behavioural measures which are indicative of the characteristics 'boldness' and 'nervousness' have been shown to be influenced by a variety of different types of early experience. For example, Wilson, Warren & Abbott (1965) found that kittens handled regularly during the first 45 days of life approached unfamiliar objects more rapidly, and spent more time in close proximity to them at 4–7 months, than did non-handled animals. Mendl (1986) demonstrated that singleton kittens, reared with their mother alone, were quicker to emerge from a nest box into an unfamiliar room at 3–7 weeks, than were kittens raised with their mother and a sibling.

Variation in 'boldness' or 'nervousness' may thus be directly related to variation in forms of early experience including the social environment and exposure to handling by humans. These aspects of early experience also have effects on other types of behaviour. For example, Mellen (1992) reported that female kittens hand-raised singly from birth by humans became much more aggressive to both humans and conspecifics than kittens raised by their mothers. Kittens raised in pairs by humans developed into moderately aggressive adults that were also 'nervous' and 'flighty'. The absence of the mother appeared to result in the development of 'aggressive' and 'unfriendly' individuals, especially if these individuals were not reared with siblings.

Further studies of the influence of human handling or 'socialisation' have demonstrated that the timing and amount of early handling that a kitten receives (Karsh, 1984), and the number of handlers a kitten



has (Collard, 1967), influence its later 'friendliness' to humans. These studies are reviewed in detail in Chapter 10. In addition to the effect of socialisation on 'friendliness', recent work has also suggested that it may affect how kittens adapt to housing in animal shelters. For example, Kessler's (1997) work indicated that cats which were not socialised towards conspecifics showed more signs of behavioural distress when group-housed in an animal shelter than did socialised individuals. The non-socialised animals seemed better able to cope when singly housed. Also, cats which were not socialised to people appeared more stressed in both single and group-housing conditions than did socialised cats.

In most of the studies described here one feature of early experience has been varied while as many others as possible have been held constant. This often results in clear differences in the subsequent behaviour of the cats, and sometimes in a near bimodal distribution of animals. However, many features of individuality are likely to show a continuous rather than a discontinuous distribution. For example, cats may be described as 'tense' and 'high-strung' or 'calm' and 'equable' or anything between. This continuity of variation probably reflects a fact that is also evident from the studies described above, namely, that many different types of early experience may exert some influence on the expression of a particular behaviour pattern at a later date. Further, it is also clear that a particular aspect of early experience may influence a number of different types of behavioural characteristic.

### Interactions between genetic and environmental sources of variation: paternal and handling effects on 'friendliness'

In this section, we examine some recent studies which have investigated how genetic and environmental factors interact to influence the development of behavioural characteristics in the cat. These studies have their roots in the work of Turner *et al.* (1986), who demonstrated that one factor which helped explain the variation in observer ratings of kitten 'friendliness' was kitten paternity. Kittens of different fathers differed significantly in their 'friendliness' scores. Since they never saw their fathers, it is likely that genetic factors mediated this effect.

Turner *et al.* (1986) observed that in one of the cat colonies they studied, the friendly father produced kittens which were more friendly, than did the less

friendly father. In the other colony, the two fathers did not differ so clearly in friendliness and yet they still produced kittens which clearly differed in this characteristic. In a more recent study, Ledger (1993) failed to find a correlation between measures of kittens' responses to humans and those of their fathers. One possible explanation for this finding is that a father's 'friendliness' when young and not when adult may be the best predictor of the 'friendliness' of his kittens. However, taken together, the findings of Turner *et al.* (1986) and Ledger (1993) indicate that evidence for direct inheritance of behaviour related to 'friendliness' is weak. As mentioned by Martin & Bateson (1988), it is important to remember that genes do not code for behaviour patterns. Rather, it is more likely that, in this case, genes from the father generate differences in behavioural characteristics by indirect routes, for example by affecting growth rate which may in turn affect socialisation to humans in a colony situation and thereby affect subsequent 'friendliness' (Turner *et al.*, 1986).

Further studies by Reisner *et al.* (1994) and McCune (1995) supported the original finding of Turner *et al.* (1986) that variation in measures of kitten 'friendliness' is partly explained by kitten paternity. In the study of Reisner *et al.*, apparent paternal effects on kitten behaviour may have been attributable to breed differences between fathers. McCune's study examined how variation in early experience of being handled affected subsequent behaviour, and how such effects were influenced by the kittens' paternity. Kittens sired by a friendly father and others by an unfriendly father were either regularly handled from weeks 5–12 of age, or not handled during this period. At one year of age, the offspring of the friendly father and those who had been handled during early life were quicker to approach a person in a test situation, and spent more time with them than the non-handled animals and the offspring of the unfriendly father. Handled and non-handled cats did not differ in their responses to a novel object, but the offspring of the friendly father were quicker to approach and explore the object than those of the unfriendly father. This last finding led McCune to suggest that the paternal effect on 'friendliness' observed in previous studies was actually a more general effect on 'boldness'. Paternity influenced a general response to unfamiliar or novel stimuli, irrespective of whether these were people or inanimate objects. This result demonstrated how detailed study

may lead to a reinterpretation of the true nature of a behavioural characteristic. Early handling, however, appeared to have a specific effect on the cat's behaviour towards humans – its 'friendliness'. There appeared to be a degree of additivity in the genetic and environmental effects on some of the cats' responses to humans. Friendly-fathered handled cats behaved in the most positive way to people, and there was some evidence that friendly-fathered unhandled and unfriendly-fathered handled cats were intermediate, with unfriendly-fathered unhandled cats behaving most negatively. McCune's study thus represents a first attempt to disentangle the interactive effects of genetic and environmental factors on individual behavioural characteristics.

### Development and cross-time consistency of individuality

The fact that variation in genetic and environmental factors can underlie variation in individual behaviour tells us little about the precise way in which behavioural characteristics actually develop across time, when and if they stabilise within individuals, and how stable they become. To address these issues, we need to conduct longitudinal studies of individuals, measuring and observing their behavioural characteristics as they develop. In Chapter 2, Bateson gives a comprehensive discussion of behavioural development in the cat. Here, we present some examples which bear directly on the problem of the development of individuality.

#### Early characteristics may not predict later characteristics: alternative routes to the same end point

Work on the development of predatory behaviour has demonstrated that early individual differences in what could be termed 'predatoriness' do not necessarily predict subsequent variation in the predatory abilities of older cats. To summarise briefly, Caro (1979a, b, 1980a, b) and Baerends-van Roon & Baerends (1979) showed that between two and three months of age, individual kittens varied considerably in predatory ability. However, by six months and on into adulthood, many of these differences had vanished, although some forms of predatory skill still varied. Thus, much of the early individual variation in kitten 'predatoriness' seemed to be a transient phenomenon

which subsequently disappeared, probably due to the effects of later experience masking or overcoming earlier ineptness in some kittens. As Bateson notes in Chapter 2, a given developmental outcome (e.g. competence as a predator) may be reached via many different types of developmental history. Perceived individual variation in aspects of behavioural style may thus sometimes be the product of 'alternative developmental routes' to the same outcome (Bateson, 1976), and may disappear in the longer term.

However, this is not the whole story. It is clear that certain forms of early experience have longer lasting effects on subsequent predatory abilities. For example, kittens that had experience of particular prey species during early life were more adept at handling and killing these species later at six months of age and did not easily generalise their skills to other species (Caro, 1980a). Thus, a characteristic of individuality such as 'predatoriness' may comprise a variety of attributes which show different properties of stability and change across time.

A similar example is provided by McCune (1992) who observed that, although friendly-fathered unhandled kittens and unfriendly-fathered handled kittens were similar in their friendliness to humans at one year of age, the latter were much more friendly at 12 weeks, just after the handling treatments had been completed. Thus, during the period between 12 weeks and one year, early differences between the two sets of individuals disappeared. Perhaps the impact of the early handling treatment wore off with time, allowing the paternal effects on 'boldness' to be expressed more strongly (McCune, 1992). Both this study and those of kitten predatory behaviour suggest that variability in individual characteristics early in life, around three months of age, may not always predict subsequent individuality in the cat.

#### Early characteristics may not predict later characteristics: the emergence of differences

Reisner *et al.* (1994) noted that when tested at eight weeks of age, kittens from different fathers did not differ in their 'friendliness' to an unfamiliar person, whereas clear differences did emerge at 20 weeks. They suggested that the novelty of the tests at eight weeks may have resulted in a state of fear in the kittens overriding any variation in behaviour due to paternity. However, differences were also not observed at 12 weeks, when the test was no longer novel. This

raises the interesting possibility that paternal effects on 'friendliness' or 'boldness' may only become expressed at a certain point of development and maturity. This might also account for McCune's (1992) finding that in friendly-fathered unhandled kittens, the paternity effect on kitten boldness did not appear to be evident at 12 weeks of age. However, it is also worth pointing out that Turner *et al.* (1986) observed clear paternal effects on their measure of kitten 'friendliness' at 3–4 months of age. Differences between the design of the studies and methods for measuring 'friendliness' may well account for some of the differing effects found. For example, Reisner *et al.* (1994) measured 'friendliness' by assessing kittens' responses to handling and also restraint, while Turner *et al.* (1986) based their measures on observer ratings of kittens in free situations. The former method is likely to have been more stressful for the kittens and hence to decrease the chance that behavioural variation due to paternity would be expressed.

More generally, there are a number of other reasons for why individual behavioural characteristics at one age may not be correlated with those at another. For example, individuals may develop at different rates and these differences may be evident at one age but not at another. The behavioural expression of particular characteristics may change with age, as may the factors controlling and functions of particular behaviours. Thus, tests which measure these behaviours and characteristics may do so reliably at one age but not at another (Hinde & Bateson, 1984). Assessing the development and emergence of individuality is therefore a difficult job which needs to be carried out with these points in mind, particularly when an apparent lack of consistency across time is detected.

### Evidence for stability of individuality across time

In contrast to the findings just discussed, some studies have detected apparent cross-time consistency in cat individual characteristics. For example, Durr & Smith (1997) showed that individual rank-ordering in latencies to approach and attention paid to novel objects or animals, measures of what could be termed 'boldness' and 'curiosity', remained reasonably stable across a five-week period. This was despite the fact that the social environments of the cats were altered each week. The cross-time consistency was most pronounced when the cats were tested in groups rather

than singly, suggesting that individual differences in behaviour in a non-social context may become amplified when individuals are allowed to interact with each other. For example, clear-cut social rankings may influence individual behaviour and underlie the consistency of the patterning of a group response.

Durr and Smith's study covered a short period of the cat's lives, but other authors have suggested stability of individual characteristics across longer time intervals. Turner *et al.* (1986) found some consistency in 'friendliness' of kittens from 3 to 8 months of age. Moelk (1979) distinguished 'slow/quiet' and 'quick/noisy' kittens in her study of friendly approach behaviour in the kitten; quick/noisy kittens were more exploratory and quickest to investigate unfamiliar stimuli. She suggested that these differences were present from birth and persisted into adulthood.

Cook & Bradshaw (1995) recorded the post-mealtime behaviour of kittens at four months, one year and two years of age. Using principal components analysis to analyse the interactive behaviour patterns recorded, three factors labelled 'active', 'rubbing' (high frequency of rubbing on objects and human), and 'inquisitive' were found to show consistency across time. The rank orderings of individuals on 'active' were positively correlated at 4 months and 1 year. The same was true for 'inquisitive', while rubbing showed some stability of inter-individual differences from 1 to 2 years. However, the apparent lack of consistency from 4 months to 2 years emphasises that these characteristics are also open to environmental influence across this period. In a subsequent study, Cook & Bradshaw (unpublished data) also found evidence of cross-time consistency from 4 to 33 months in measures of escape behaviour shown by kittens when being handled.

### Do constitutional physiological differences underlie stable individual characteristics?

The existence of individual variation in characteristics such as 'timidity' and 'boldness', at, or shortly after birth, has been noted in species other than the domestic cat, and related to so-called constitutional differences in the physiological characteristics of the individuals. For example, Suomi (1983, 1987) found that young rhesus monkeys varied in the magnitude of physiological response shown (e.g. heart-rate changes) to various situations, and that these responses were related to the behaviour shown

in mildly stressful situations later in development. In wolves, the dominant cub in a litter (as defined in behavioural tests and observation) was found to differ from its littermates in heart-rate and other autonomic measures in particular test situations (Folk, Fox & Folk, 1970; Fox, 1972; Fox & Andrews, 1973). Lyons *et al.* (1988) found that persistent individual differences in timidity were associated with differences in pituitary-adrenal responsiveness in dairy goats. More recently, studies of wild house mice have also indicated that there may be physiological correlates to apparently stable differences in a suite of behavioural characteristics such as 'aggressiveness' and 'activity' (Benus *et al.*, 1991).

It is tempting to suggest that if a behavioural characteristic has a physiological correlate, then it must be a stable feature of the animal. However, physiological systems change with time and situation as do behavioural ones, and the relationship between measures of behaviour and physiology may only be apparent under certain circumstances (e.g. Suomi, 1987; Kagan, Reznick & Snidman, 1988; see Mendl & Deag, 1995). The discovery of physiological correlates of individual differences in behaviour provides us with a further tool for studying the development of such differences. It may be possible to demonstrate a physiological basis for certain aspects of individuality, particularly those that appear to be present at birth, and to relate behavioural stability across time to stability at the level of physiological systems.

### Is cat individuality stable across situations?

A major issue in the study of human temperament is the extent to which temperament is a feature of the person or the situation (Stevenson-Hinde, 1986; Goldsmith *et al.*, 1987). This issue is often examined through an assessment of the cross-situational consistency of particular temperamental characteristics. Stevenson-Hinde (1986) suggested that some aspects of temperament may be thought of as lying at one end of a 'person-situation' continuum while others lie at the other end or at points ranging in between. Thus, activity may be nearer the person end (relatively unaffected by situation or context) than negative mood (more dependent upon the situation). In studies of cat behaviour, there is also evidence that certain measures of behaviour change quite dramatically according to the context in which they are observed while others are less labile.

### Context effects on individual behaviour

Rochlitz, Podberscek & Broom (1998) used questionnaires to assess owners' ratings of their cats' behaviour at different times before, during and after a period of quarantine. The owners reported that midway through quarantine, the cats were less 'relaxed' and 'playful', and more 'aggressive' and 'nervous', than prior to quarantine. At release from quarantine, the owners rated their cats as more 'friendly', 'affectionate' and 'timid', and three months later as more 'affectionate', 'nervous' and 'vocal' than before quarantine. The results suggest that the experience of quarantine had an effect on measures of cat individuality, but there are alternative explanations. The interactions that the owners could have with their cats were much more restricted in the small quarantine cages than at home (Rochlitz *et al.*, 1998). The owners themselves experienced changes in their relationships with their pets, may also have had expectations of how quarantine would affect the cats, and may have altered their behaviour and perceptions accordingly. Time as well as context changed during the study. Nevertheless, it is plausible that at least some of the changes observed reflected true changes in cat individuality, and further studies could build on these findings by complementing owner reports with other forms of measurement. The study also emphasises that important real-life contextual changes such as moving house, and being quarantined or housed in a cattery, may result in changes in a cat's behavioural style. How long-lasting such changes may be is a subject for further research.

Using standardised tests of behaviour, Cole & Shafer (1966) also showed how context could dramatically affect measures of a cat's individual characteristics. They performed two tests of competitive ability. In one test two cats were placed together to compete for one food reward while in the other several animals had to compete for access to a food bowl from which only one animal could feed at a time. The authors found that reliable dominance hierarchies (in terms of access to the food) developed in both tests, but that they differed between the two tests. For example, one of the most 'aloof', 'placid' and low-ranking cats in the group test was actually the most 'aggressive', 'energetic' and dominant in the two-cat test. The context of the test situation had a marked effect on the behaviour seen in social competition, even by the same individuals.

The above examples involve aspects of behavioural style which are measured through an assessment of relationships between cats (and between cats and people). These may be especially open to contextual influences because, in social situations, the behaviour of others has strong effects on an individual's own behaviour (Hinde, 1979). Furthermore, individuals may also develop complicated context-specific ways of behaving according to past experience with other individuals which act to mask or constrain the expression of any underlying stable behavioural characteristics (see Mendl & Deag, 1995).

A final example of contextual effects on individuality refers to the 'internal context' or internal (e.g. hormonal) state of the animal. Certain mothers who are usually very friendly to humans become extremely hostile once they give birth (personal observation). The presence of young kittens and the onset of lactation appears to induce a more 'protective' and 'defensive' style of behaviour that overrides their previous 'friendliness'. This dramatic change in behaviour makes adaptive sense and is common in mammals (Maestriperi, 1992). Mothers should defend their offspring from potential predators. The most interesting aspect of this observation is that only some mothers show this change. Others remain as friendly as before they gave birth (personal observation). Thus, although changes associated with parturition and lactation may underlie shifts in behavioural style, there also appears to be individual variation in the extent of these shifts; maternal behaviour itself varies between individual cats (Lawrence, 1981; Feldman, 1993). A similar finding comes from studies of the effects of castration on the behaviour of male cats. While it is clear that castration often results in dramatic changes in behaviour such as 'aggressiveness' and 'docility', there is marked individual variation in the extent of behavioural changes shown as a result of this hormonal manipulation (Hart & Eckstein, 1997).

#### Responses to novelty or unfamiliarity: 'cross-context' stability?

If stable behavioural characteristics exist, it could be argued that they are most likely to be expressed in contexts where the animal has no prior knowledge of the circumstances (Mendl & Deag, 1995). Under conditions where the animal has no expectations or learnt rules about how to respond, it needs to revert to any underlying behavioural predispositions it might

have. Such situations include encounters with novel or unfamiliar stimuli and circumstances, and it makes adaptive sense for an animal to respond in this 'automatic' way, allowing it to direct full attention to these potentially dangerous situations rather than to organising and moderating its behaviour according to previously learnt rules (cf. Fentress, 1976; Mendl & Deag, 1995).

If this argument is correct, one might expect a high degree of consistency of individual behavioural responses in novel, unfamiliar or challenging situations. In fact, much of the research on individual differences in behaviour has involved using tests of this sort to examine 'boldness', 'fearfulness', 'timidity', 'emotionality' and so on, perhaps because these tests do indeed tend to produce consistent individual differences (see Sloan-Wilson *et al.*, 1994). Although consistency may be observed in apparently different situations, if all these situations have a similar feature in common (e.g. exposure to novelty), it is questionable whether this can be referred to as 'cross-context' consistency because the underlying motivation in these situations remains the same (cf. Jensen, 1995).

In the cat, Durr & Smith (1997) showed cross-time consistency in the behaviour of cats in a number of different tests of response to novelty and unfamiliarity. Cross-situation stability was not formally assessed in this study, but the authors did calculate a median score for each cat across all tests types implying that there was some consistency across tests.

Bradshaw & Cook (1996) studied the organisation of specific behavioural actions made by cats before and after a meal. They found that cats showed individual behavioural styles around feeding, although different behaviours were expressed differently in the pre- and post-feeding contexts. However, behaviours directed towards the unfamiliar observer appeared to show some consistency across both contexts, perhaps due to the novelty of the stranger's presence at meal-time. So, there is limited support for the idea that the same individual may exhibit similar behaviour in various unfamiliar or novel contexts. However, much more evidence is needed to confirm this hypothesis in cats.

#### Are there different types of individuality in the cat?

Throughout our review, we have used adjectives such as 'friendly' or 'curious' in a colloquial way to indicate

the various dimensions of individuality in the cat that have been studied. Is there any evidence that the behaviours studied can be categorised under a limited number of major headings, as is attempted in studies of human personality and temperament? Feaver *et al.* (1986) rated cats on a wide range of different types of behavioural style and from these came the three uncorrelated dimensions of 'alert', 'sociable' and 'equable'. There are certainly some similarities between these dimensions and those found in studies of child temperament (e.g. activity, sociability, emotionality: Buss & Plomin, 1986) and personality in other species (e.g. Stevenson-Hinde *et al.*, 1980a; Mather & Anderson, 1993; Sloan-Wilson *et al.*, 1994; see above). It is thus possible that, in a variety of species, individual differences in the propensity to be active/reactive, sociable and calm may underlie many of the behavioural differences seen between individuals. However, it must be remembered that emergent dimensions depend entirely on the types of behaviours recorded, and if studies focus on similar types of behaviour (e.g. Feaver *et al.*, 1986 and Stevenson-Hinde *et al.*, 1980a), this may increase the chance of similar dimensions being detected.

Feaver *et al.* (1986) identified a number of different types of cat according to their scores on the different dimensions. There were active/aggressive cats, timid/nervous animals, and confident/easy-going animals (Feaver *et al.*, 1986). However, some profiles of individual cats did not fit into these groupings emphasising that there is unlikely to be a limited number of easily definable cat personality types. Nevertheless, Karsh & Turner (1988) argued that other researchers have also identified similar cat types. This may indicate that such types of cats are indeed prevalent in the population, or it may reflect researchers' interests in particular forms of cat behaviour.

Differences along the dimension of activity have also been reported in studies of cats faced with a challenging situation, such as being placed in a cattery or in quarantine. Kessler (1997) reported that some individuals moved around a lot while others remained inactive and tended to hide. McCune (1992) mentioned similar findings. Whether these response types are similar to the active and passive coping styles recently identified in rodents (Benus *et al.*, 1991) remains a subject for further research.

Finally, and more generally, the question of whether cat individuality varies in a discontinuous way with discrete groupings of particular individual

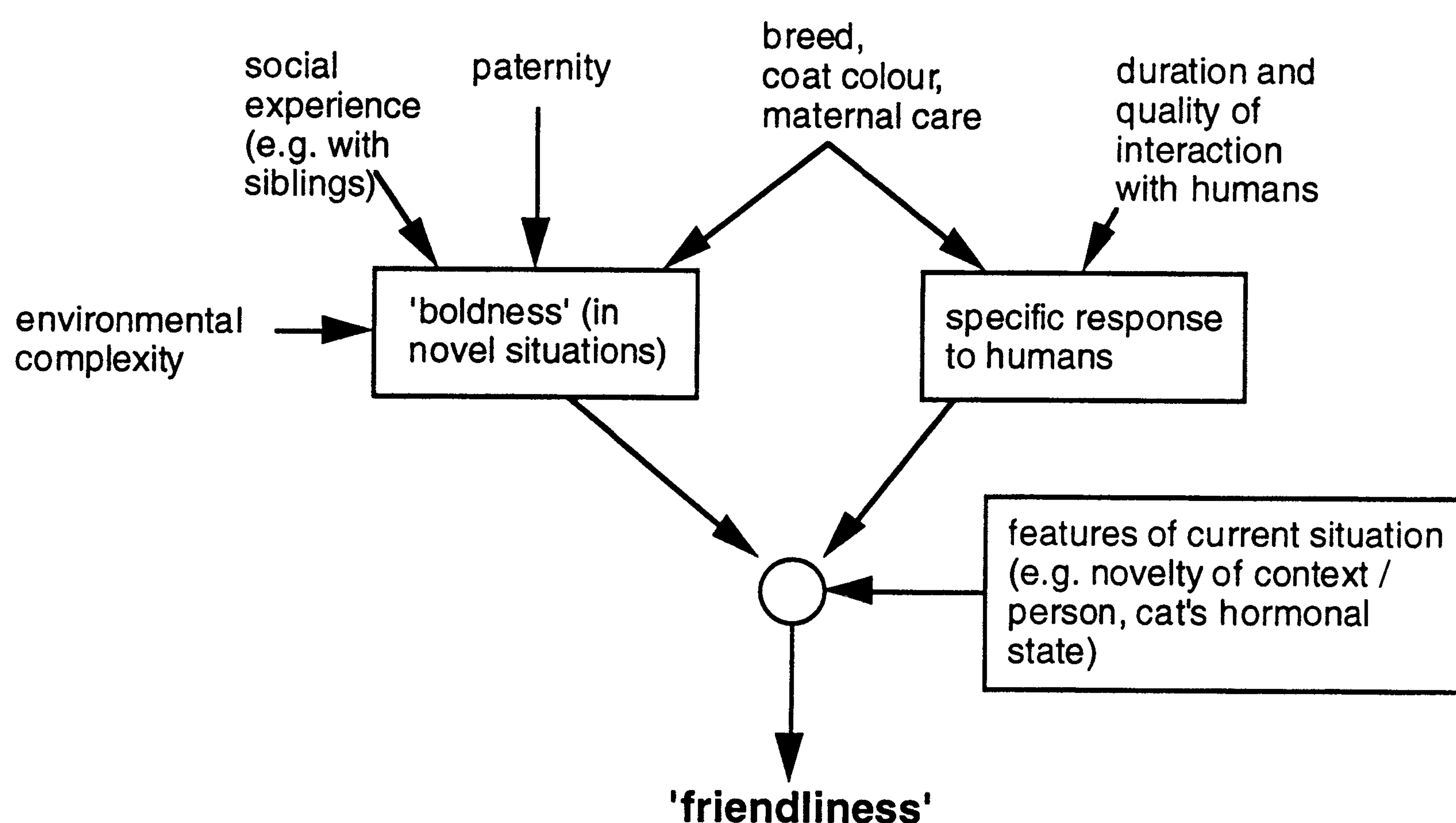
types (e.g. Meier & Turner, 1985), or whether there is a continuous range of variation between extremes, also remains to be answered. Many studies do not report whether the actual distribution of characteristics is continuous or, for example, bimodal (cf. Jensen, 1995).

### Concluding remarks

Since our original paper on individuality in the cat (Mendl & Harcourt, 1988), a number of new studies have been published which have, in particular, provided new information about the origins, development and stability of this phenomenon. Evidence of links between breed differences and behavioural style, and between patination, coat colour and temperament, suggest that at least some aspects of individuality are linked to the actions of genes. Perhaps most importantly, new studies have confirmed the effects of paternity on kitten 'friendliness to humans' first discovered by Turner *et al.* (1986), and have suggested that these effects may actually be on a more general characteristic such as 'boldness' (McCune, 1995). It is also clear that different types of early experience influence the behavioural style of adults. The size of the litter a kitten is raised in and the degree of exposure to humans during development both have effects on several aspects of temperament, including 'friendliness' and 'boldness'. McCune's (1992, 1995) studies examining the effects of paternity and early experience on these characteristics have made a start at teasing apart the effects of genetic and environmental factors on individual traits. Studies of cross-fostered kittens may illuminate this issue further.

Of all the characteristics studied, 'friendliness to humans' has received most attention. Figure 4.2 summarises some of the factors which appear to affect the expression of this behaviour, based on studies which we have reviewed here. The expression of friendliness may be the result of an interaction between an individual's general 'boldness' in novel or challenging situations, its specific attraction to humans, both of which are affected by a variety of factors, and features of the current situation. Undoubtedly, the schema illustrated in Figure 4.2 is over-simplistic but it nevertheless illustrates the complex nature of the origin and development of individuality.

Despite the progress that has been made, many questions remain largely unanswered. The mecha-



**Figure 4.2.** A schematic representation based on studies of cat individuality of some of the factors that may influence the behavioural characteristic of 'friendliness to humans'. See text for details.

nisms by which genes influence the behavioural traits of cats are poorly understood. It is also unclear whether there are a limited number of basic dimensions of cat individuality, and what these are. The cross-time and context stability of individual characteristics is still something of a mystery. There is evidence that characteristics such as 'boldness' and 'reactivity' show some cross-time stability even from an early age, while characteristics such as 'predatoriness' and 'friendliness' may be less stable during early life. However, stability over a few short weeks, or even over a 12-month period, is a very different proposition from lifetime retention of a trait. Similarly, the evidence for cross-situational stability is not strong. Whether this is because changes in behaviour in different contexts mask underlying propensities, or that these propensities are solely a function of context, awaits further analysis. Finally, the consequences of individuality in the cat have received little attention. However, the recent work by Pontier *et al.* (1995), linking coat colour variation, individual behaviour traits, and gene frequencies in populations, is an important start to this line of research, and work examining how different behavioural styles help cats to cope with caging or quarantine represents a new approach to understanding consequences which has important implications for animal welfare.

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