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The impact of paternity and early socialisation on the development of cats' behaviour to people and novel objects

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Abstract

A developmental study in domestic cats (*Felis silvestris catus*) examined the interaction of their early socialisation and the friendliness of their father and its consequences on their later friendliness to people. Kittens were either handled between 2 and 12 weeks of age (socialised) or received no handling (unsocialised) during this period. These kittens were the offspring of either a 'friendly' father or an 'unfriendly' father. When 1 year old, these cats went through a series of three experiments: (1) response to a familiar person; (2) response to a stranger; and (3) response to a novel object. Cats socialised or from the friendly father were quicker to approach, touch and rub a test person, were more vocal and spent a greater total time within 1 m of them. Differences in the cats' response to a novel object could not be accounted for by differences in early socialisation. However, cats from the friendly father were quicker to approach, touch, explore and remain in close contact with the novel object than were cats from the unfriendly father. The genetic contribution to friendliness towards people in cats was reinterpreted as boldness; a general response to unfamiliar or novel objects irrespective of whether or not the objects are people. The socialisation effect was specific to the cats' response to people. Socialised cats and friendly-fathered cats were not only friendlier to unfamiliar people but less distressed when approached and handled by them.

Keywords: Cat; Behaviour; Socialisation; Paternity; Temperament; Novelty; Animal welfare

1. Introduction

Domestic cats show enormous individual variation in their behaviour towards people. Distinct personality types are recognised in their pets by most cat owners but only relatively

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recently have ethologists turned to the cat for studies of individual differences (Feaver et al., 1986; Turner et al., 1986; Mendl and Harcourt, 1988; Karsh and Turner, 1988; McCune, 1992). Friendliness of cats towards people is one of the areas that has received attention in the study of individual differences. A study by Feaver et al. (1986) found that traits such as 'friendliness to people', defined as 'willingness to initiate proximity and/or contact' could be reliably ranked by people who knew the cats and who showed high inter-observer reliability ($n=14$, $rs=0.91$, $P<0.005$). Such global assessments of friendliness also correlated well ($n=14$, $rs=0.69$, $P<0.01$) with the rank order resulting from measured behaviour towards people (approaches by the cat, sniffing the person, head and body rubs). Various studies have identified sources of individual variation in cats' behaviour towards people. Early socialisation particularly within the first 12 weeks of life, was found to increase a kitten's willingness to approach people (Wilson et al., 1965; Karsh, 1983, 1984) and to remain held by a person (Karsh, 1983, 1984). The age when handling occurs (Karsh, 1984; Karsh and Turner, 1988), the amount of handling received (Wilson et al., 1965; Karsh, 1984), the number of handlers (Collard, 1967, although see Karsh and Turner, 1988) and the style of handling (Wenzel, 1959 cited by Rosenblatt and Schneirla, 1962; Moelk, 1979; Hurni and Rossbach, 1987) all influence the cat's degree of friendliness towards people later in life. The one handling study in disagreement with this general result is Turner's paper (1985) where he presented preliminary findings of a study on cat behaviour towards strangers, but this is explained by the handling being received when the cats were adult and not during their peak socialisation period (personal communication, 1993). There is some suggestion in the literature that the effects of on-going handling are less robust than early handling (Karsh and Turner, 1988) and indeed kittens not handled during this peak period of socialisation rarely become friendly to people later in life.

Turner and his co-workers (1986) were able to account for the friendliness rankings in a cat colony by the friendliness of each kitten's father. Friendly-ranked kittens were disproportionately distributed between two fathers, one of which was extremely friendly and the other very unfriendly. As the kittens had never seen their father, they concluded the effect was genetically mediated. Reisner et al. (1994) also found an effect of kitten's father on the time spent close to a test person, in litters sired by five different fathers. Fält (1984) demonstrated a sire effect in the willingness of puppies to make contact with a person.

None of the early handling studies manipulated genetic differences. This is the first study to look simultaneously at kittens' early socialisation to people and the friendliness of their father, enabling the interaction of these two effects to be teased apart. Variation produced by these manipulations was used as a basis for exploring differences in the cats' responses to a familiar person. A second experiment examined whether differences in friendliness extended to unfamiliar people. The third experiment examined the cat's response to a novel object and was designed to tease apart the general response of cats to novel objects from their response to people. Two predictions were posed: (1) if the response to people is just part of a wider response to novelty, of which a test person is just one type of novel object, then differences between treatment groups observed in the first two experiments would also be expected in the novel box test; (2) if the response is not part of a wider response to novelty, then differences between cats observed in the first two experiments would not be expected in the novel box test.

2. Methods

The study was carried out at the Sub-Department of Animal Behaviour at Madingley, University of Cambridge. Thirty-seven kittens (domestic short-hair variety) were used in the study; 19 males and 18 females, born to eight mothers and two fathers, in 12 different litters. Mothers were unrelated to the two fathers. Two of the mothers were distantly related; all others were unrelated.

Shortly after parturition, mothers and their kittens were moved to an adjoining nursery area where they were housed as separate family groups until the litter was 12 weeks old. Each mother and litter were provided with ad libitum water and food (80% Whiskas Supermeat and 20% Purina, by volume). Litters were visually separated from each other in the nursery area although some auditory and olfactory contact was possible. These nursery rooms were later used as test rooms (Fig. 1) when the kittens had reached a year of age. One-way viewing enabled subjects in the room to be observed from outside the room without detection.

At 12 weeks of age, the kittens were sexed, photographed, weighed, vaccinated (against Feline Respiratory Virus Disease and Panleukopenia) and moved to single sex rooms in an adjacent area of the cat house. Mothers were returned to a third room which housed the non-breeding and pregnant females. Fathers were individually housed. All home pens consisted of an indoor room and an outdoor run to which cats had continuous access through

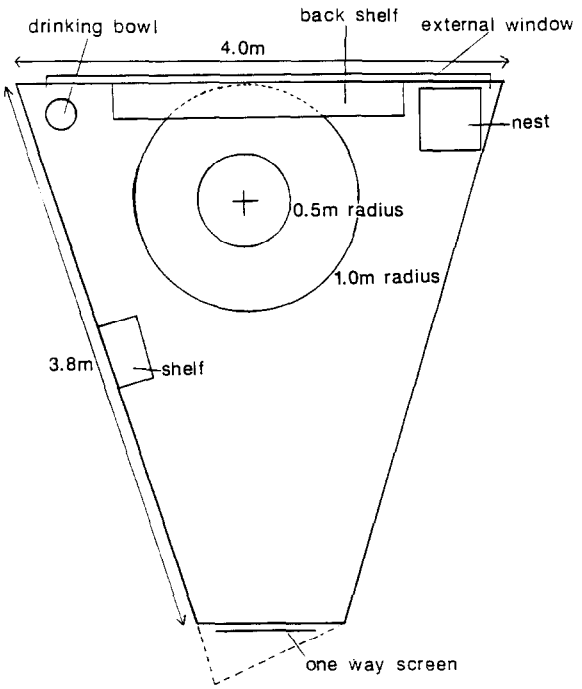

Fig. 1. Plan of a test room.

a catflap. Complexity was provided in the home pens by using logs, scratch-posts, shelving and toys in addition to nestbeds, littertrays and containers for food and water.

2.1. Experimental manipulation

Litters were randomly assigned in advance to one of four experimental groups, according to differences in friendliness of father and early handling experience. The four groups were: (i) friendly-fathered/socialised (FS); (ii) friendly-fathered/unsocialised (F/US); (iii) unfriendly-fathered/socialised (UF/S); (iv) unfriendly-fathered/unsocialised (UF/US).

Half of the kittens were sired by the 'friendly' father and half by the 'unfriendly' father. Both fathers were still available from an earlier study (Turner et al., 1986) carried out at the same site, where 'friendliness' had been defined as latency to initiate proximity and/or contact with people. On a person's approach, the 'friendly' father would typically approach immediately showing all the signs of greeting: tail raised, kneading his paws, rubbing the person and drooling. In contrast, on the approach of a person, the 'unfriendly' father would retreat to the back of the pen, adopt a flattened posture, with tail tucked under him, head lowered and avoid eye contact.

In this study, socialisation refers to cat–human contact and not cat–cat contact. Unsocialised kittens were only exposed to people during the daily routines of cleaning and feeding. The technician minimised his interference and contact with all kittens. In socialised litters, kittens were handled from 2 weeks of age through to 12 weeks of age. Kittens were placed onto the handler's lap and had their head and body petted while being spoken to gently. Each litter received a weekly total of 5 h of handling, spread across as many days as possible but at least 5 out of each 7 days. Each kitten was handled for the same length of time per session. Mothers stayed in the room during socialisation. Rodel (1986, cited by Karsh and Turner, 1988) says the mother's presence may have an effect, where she is friendly (as were most of the colony mothers) the mother may facilitate the establishment of a relationship. The mother was left in the room rather than risk effects of separation distress. All kittens were moved from their nursery room to their home pens at 12 weeks of age.

2.2. Behavioural observations

At a year of age, cats went through a series of three experiments: (1) the Familiar Person Approach Test (FAT); (2) the Stranger Approach Test (SAT); and (3) the Novel Box Test. The series was designed to test for differences between cats in their response to meeting and being handled by people and for their reaction to a novel object.

Variables used in the tests are defined in Table 1. Subjects were tested over the course of 3 consecutive days, once each morning (between 09:00 and 12:00 h) and once each afternoon (between 14:00 and 17:00 h) so that each test was conducted twice. Differences between morning and afternoon data were non-significant and therefore lumped to give a single data point.

Cats were taken in a carry basket to the test room, which had been emptied of 'furniture', and were left to habituate for 30 min (Fig. 1). Behaviour was recorded as follows: (i) at the time of entry by the test person. As the test person entered and approached the chair, the cat's gross behaviour was recorded with one–zero sampling on a checksheet using a

Table 1
Definitions of test variables

Variable	Definition
Latency to emerge	No. of seconds before cat places all four feet on ground outside the carry basket
Latency to 1 m	No. of seconds before most of the cat's body is inside the 1 m radius circle taped on the floor
Latency to 50 cm	No. of seconds before most of the cat's body is inside the 50 cm radius circle taped on the floor
Latency to touch	No. of seconds before the test person or novel object is first touched
Latency to rub	No. of seconds before the test person or novel box is first rubbed
No. of rubs	No. of times the test person or novel box is rubbed
No. of times in box	No. of times inside the novel box (entry is most of body inside novel box)
Part body in box	No. of seconds before part of body is inside the novel box
Whole body in box	No. of seconds before most of body is inside the novel box
Total time in box	No. of seconds when most of body is inside the novel box
Total time < 1 m	No. of seconds when most of body is inside the 1 m radius circle
No. of vocalisations	Number of separate vocalisations uttered by cat
Hiding	Cat partly hidden by nest bedding or retreated behind nest
Escape attempts	Cat makes desperate attempt to leave the test room
Flattened posture	Body and head posture lowered, in close contact with the ground; stiff appearance
Knead paws	Cat treads its paws combined with other friendly behaviour

Hiss, growl, purr, arch back (defined as back curve), tail up, body roll, rub person (see rub cat) and rub object are defined in the ethogram by the U.K. Cat Behaviour Working Group (1995).

series of behavioural categories (Table 1); (ii) during a 10 min test period for all three tests. A timer was started as the test person sat on the chair. Continuous recording yielded: latency measures to approach; touch and rub; the number of rubs and vocalisations made, and the total time spent within 1 m of the object or person; (iii) after the 10 min test, the test person approached to within 50 cm of the cat and recorded the cat's gross behaviour for 60 s using the series of behavioural codes; (iv) after the 60 s approach test, when the cat was stroked three times. The cat's gross behaviour was recorded using the series of behavioural categories.

Measures were recorded by the author, being the familiar person, inside the room during the Familiar Person Approach Test but recorded from outside the test room during the Stranger Approach Test and the Novel Box Test.

The FAT explored what variation in cats' responses to a familiar person could be accounted for by the friendliness of the cat's father and the cat's early handling experience.

In the SAT, an unfamiliar person replaced the familiar test person, Mertens and Turner (1988) mention that a stranger's behaviour in a test situation influences the cat's response to them. For this reason, test persons were given standard instructions not to interfere or respond to the cat during the test but to enter, move directly to the central chair and to sit down facing but not staring at the subject. No statistical differences were found according to the individual identity or gender of the stranger. Mertens and Turner (1988) found that if the stranger ignored the cat, longer latencies to approach were recorded. In this study, to avoid long latencies within a relatively short test period (10 min), strangers greeted the cat on entry to the test room and again when they approached and stroked it.

In the Novel Box Test, the test person was replaced by a novel object; an unfamiliar wooden box (45 cm × 45 cm × 60 cm). The box had two doorways and a partition dividing the interior so that cats could pass in one side of the box and out the other. The time taken for the cat to emerge from its carry basket was recorded during habituation. After 30 min habituation, I entered and placed the novel box over the central 'x' in the test room and removed the cat basket. The Novel Box Test was limited to a 10 min test period and at no stage was the cat approached.

In studies using litters, the mean litter value is usually taken as a single data point, because data points from littermates cannot be considered independent of each other. However, domestic cats are renowned for their enormous degree of individual variation. Barrett and Bateson's formula (1978) was used to assess variation within and between litters (McCune, 1992). For each variable, individual kitten means were used only if the variation within litters was at least as great as the variation between litters. Otherwise litter means were used.

As data were non-normally distributed, non-parametric statistics were used whenever possible. Two-factor ANOVA was used to look at interactions between father's friendliness and early handling experience. Although strictly speaking ANOVA should not be used on non-normally distributed data, it was selected here because an appropriate non-parametric equivalent, which could examine interactions, was not available. Significant interactions were always re-analysed as two separate tests with non-parametric methods. In the few cases where non-parametric analyses did not confirm results by ANOVA, the results were not considered.

Where an interaction of the two effects was significant, pairwise analyses of differences between the four treatment groups were conducted by non-parametric means (Mann–Whitney test and the chi-squared test using the G-statistic) to identify where most of the deviation lay from a random distribution of data.

Coded data (collected by one–zero sampling) were analysed by using the G-statistic as data violated the assumptions of the chi-squared test in that more than 20% of the expected values were less than five (Zar, 1984). For those measures where the data violated the chi-squared statistic assumptions, the log-likelihood method proposed by Wilkes (1935, cited by Zar, 1984) for assessing goodness of fit was used.

3. Results

The results of the familiar person approach test (FAT) are listed in Table 2. The FAT data show that cats could be statistically distinguished by the friendliness of their father and their early socialisation experience.

Socialised cats and cats sired by the 'friendly' father were significantly quicker to approach, touch and rub the familiar test person, were more vocal and spent longer within 1 m of the person than cats from the 'unfriendly' father.

Interactions of the two effects were significant for latency to approach within 50 cm, to touch, rub and remain within 1 m of the test person (Table 2). Where the interaction was significant (Fig. 2), friendly-fathered socialised cats (F/S) accounted for most of the deviation from a random distribution of data. They were quicker than other groups to approach the test person (<1 m: $U=29$, $P<0.001$; <50 cm $U=27$, $P<0.001$), to touch

Table 2
Familiar Person Approach Test: effects of father's friendliness and early handling experience

(i) ANOVA	Father effect (d.f. = 1)			Handling effect (d.f. = 1)			Interaction	
Variable	*F*-value	*P*-value	Direction	*F*-value	*P*-value	Direction	*F*-value	*P*-value
Latency to 1 m	15.89	0.0	F < UF	8.65	0.01	S < US	2.89	0.1
Latency to 50 cm	17.61	0.0	F < UF	9.34	0.01	S < US	4.97	0.05
Latency to touch	10.22	0.01	F < UF	14.62	0.0	S < US	7.73	0.01
Latency to rub	10.08	0.01	F < UF	12.88	0.01	S < US	7.66	0.01
No. of rubs	2.93	0.1	F > UF	–	N/S	–	–	N/S
Total time < 1 m	16.24	0.0	F > UF	8.73	0.01	S > US	4.21	0.05
No. of vocals[a]	6.3	0.05	F > UF	8.4	0.03	S > US	–	N/S
(ii) *G*-statistic	Father effect (d.f. = 1)			Handling effect (d.f. = 1)			4 Groups (d.f. = 3)	
Variable	*G*-statistic	*P*-value	Direction	*G*-statistic	*P*-value	Direction	*G*-statistic	*P*-value
Hiss	5.51	0.05	F < UF	5.1	0.05	S < US	12.13	0.05
Growl	–	N/S	–	3	0.1	S < US	–	N/S
Flat posture	9.17	0.05	F < UF	4.1	0.05	S < US	–	N/S
Hiding	5.46	0.05	F < UF	–	N/S	–	8.11	0.05
Purr	–	N/S	–	3.26	0.1	S > US	–	N/S
Arch back	4.8	0.05	F > UF	13.28	0.0	S > US	14.63	0.01
Knead paws	4.88	0.05	F > UF	5.37	0.05	S > US	10.06	0.05
Tail up	4.8	0.05	F > UF	7.53	0.01	S > US	14.63	0.01
Body roll	6.51	0.05	F > UF	4.64	0.05	S > US	13.35	0.01
Rub person	6.83	0.01	F > UF	5.96	0.05	S > US	–	N/S

[a] $n = 12$ (litter means), otherwise $n = 37$ (individual means). N/S, $P > 0.1$ hiss: $G = 5.51$, $P < 0.05$, F < UF is interpreted as friendly-fathered cats were significantly less likely than unfriendly-fathered cats to hiss at the test person.

them ($U = 36$, $P < 0.001$), rub them ($U = 34$, $P < 0.001$) and to remain close to them for longer (< 1 m: $U = 25$, $P < 0.001$).

Both friendly-fathered cats and socialised cats were less likely to hiss or adopt a flattened posture (Table 2). Friendly-fathered cats were also less likely to hide. Relaxed behaviour, associated with a lack of distress was more likely in friendly-fathered cats and socialised cats: raised tail; arched back; knead paws; rub the test person; and body roll.

Distribution of data within the four treatment groups for the variable 'Hiss' fell into three statistically distinct groups (Fig. 3). Unfriendly-fathered unsocialised (UF/US) cats were the most likely to hiss at the test person ($G = 11.05$, d.f. = 1, $P < 0.001$) while friendly-fathered socialised (F/S) cats were least likely to hiss ($G = 3.93$, $P < 0.05$). Friendly-fathered unsocialised (F/US) cats and unfriendly-fathered socialised (UF/S) cats were indistinguishable from each other but distinguishable from unfriendly-fathered unsocialised (UF/US) cats ($G = 8.15$, d.f. = 1, $P < 0.005$) and friendly-fathered socialised (F/S) cats ($G = 5.99$, d.f. = 1, $P < 0.025$).

For all other variables recorded by one–zero sampling with a significant interaction, friendly-fathered socialised (F/S) cats accounted for most of the deviation from a random distribution of data. (Fig 4). They were more likely than other groups to knead their paws

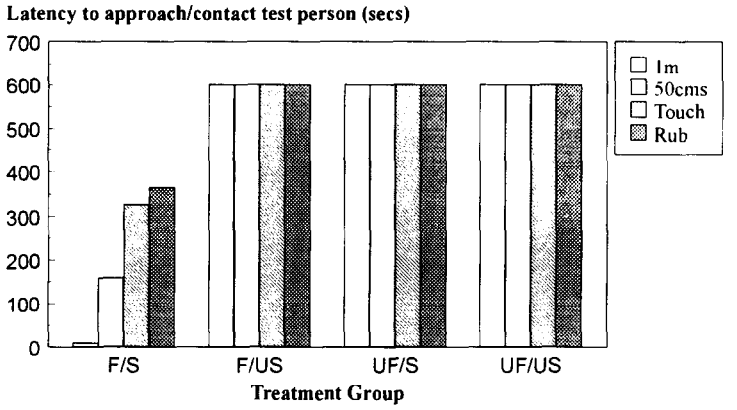

Fig. 2. Distribution of median data from familiar person approach tests within treatment groups ($n = 37$, individual medians). Latencies of 600 s represent the time limit of the test, not the start of behaviour. F/S, friendly-fathered socialised; F/US, friendly-fathered unsocialised; UF/S, unfriendly-fathered socialised; UF/US, unfriendly-fathered unsocialised.

($G = 10.13$, d.f. $= 1$, $P < 0.005$), body roll ($G = 13.20$, d.f. $= 1$, $P < 0.001$), arch their back ($G = 12.39$, d.f. $= 1$, $P < 0.001$) and raise their tail ($G = 13.15$, d.f. $= 1$, $P < 0.001$) and were less likely to hide ($G = 6.81$, d.f. $= 1$, $P < 0.01$).

Analysis of the SAT data (Table 3) yielded similar results to the FAT analysis. Socialised cats and friendly-fathered cats were quicker to approach and touch the unfamiliar test person and spent longer within 1 m of them (Table 3). Socialised cats were also quicker to rub the test person and were more vocal, (Table 3).

Only one interaction was significant: latency to approach within 1 m of the test person. Friendly-fathered socialised (F/S) cats accounted for most of the deviation from a random

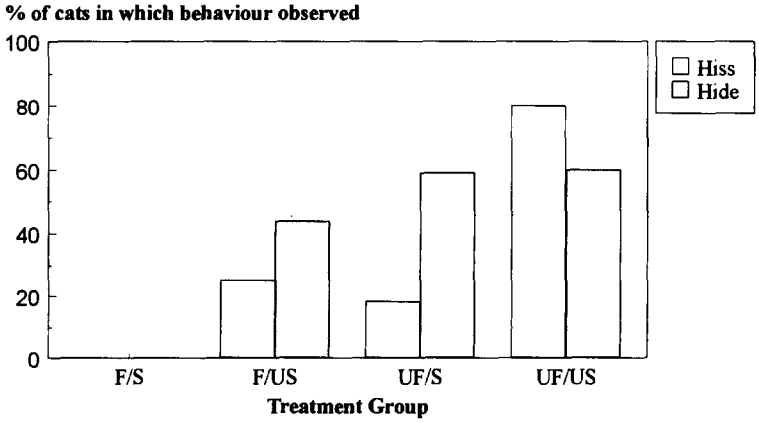

Fig. 3. Distribution of familiar person approach test data within treatment groups (G-statistic, d.f. $= 3$, $n = 37$). F/S, friendly-fathered socialised; F/US, friendly-fathered unsocialised; UF/S, unfriendly-fathered socialised; UF/US, unfriendly-fathered unsocialised.

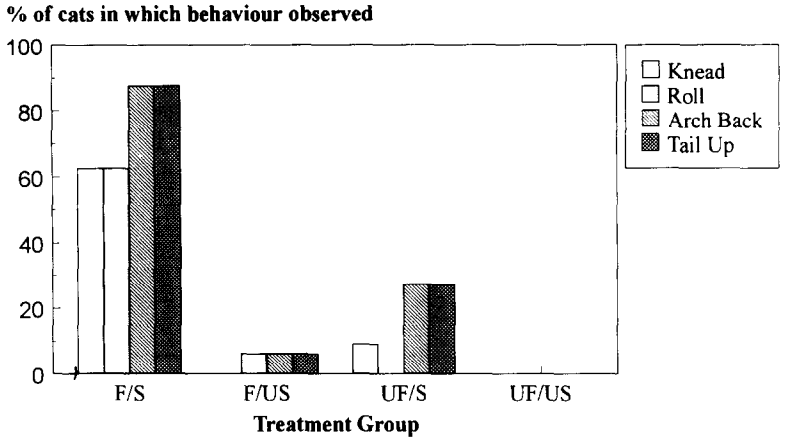

Fig. 4. Distribution of familiar person approach test data within treatment groups (G-statistic, d.f. = 3, $n = 37$). F/S, friendly-fathered socialised; F/US, friendly-fathered unsocialised; UF/S, unfriendly-fathered socialised; UF/US, unfriendly-fathered unsocialised.

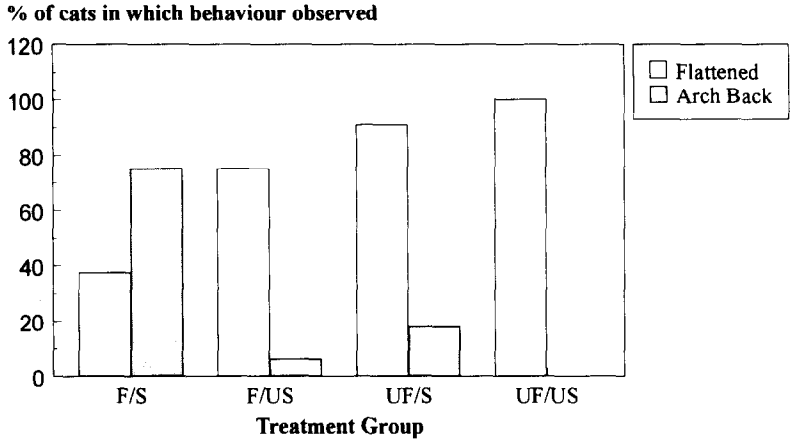

Fig. 5. Distribution of stranger approach test data within treatment groups (G-statistic, d.f. = 3, $n = 37$).

distribution of data. They were quicker than other groups to approach to within 1 m ($U = 27$, median = 1.5 s vs. rest = 600 s, $P < 0.001$) and within 50 cm ($U = 39.5$, $P < 0.001$, F/S median = 304.25 s vs. rest = 600 s) of the test person and remained within 1 m of them for longer ($U = 27.5$, $P < 0.001$, F/S median = 347 s vs. rest = 0 s). Latencies to touch ($U = 1$, $P < 0.01$) and rub ($U = 1$, $P < 0.01$) the test person were shorter for friendly-fathered socialised (F/S) litters.

Friendliness of father and early handling experience also accounted for differences between cats in their defensive behaviour (Table 3). Cats were less likely to show defensive behaviour to a stranger if they had a 'friendly' father: hiss, hide and flattened posture. They were also more likely to show relaxed behaviour: to arch their back, an element of the cat's

Table 3
Stranger Approach Test: effects of father's friendliness and early handling experience

(i) ANOVA	Father effect (d.f. = 1)			Handling effect (d.f. = 1)			Interaction	
Variable	*F*-value	*P*-value	Direction	*F*-value	*P*-value	Direction	*F*-value	*P*-value
Latency to 1 m	17.29	0.0	F<UF	17.42	0.0	S<US	7.03	0.03
Latency to 50 cm	10.71	0.01	F<UF	8.07	0.01	S<US	3.59	0.1
Latency to touch[a]	4.51	0.1	F<UF	13.16	0.01	S<US	4.51	0.1
Latency to rub[a]	–	N/S	–	8.34	0.03	S<US	–	N/S
No. of rubs[a]	3.84	0.1	F>UF	4.47	0.1	S>US	3.84	0.1
Total time < 1 m	12.68	0.01	F>UF	7.03	0.03	S>US	3.54	0.1
No. of vocals[a]	–	N/S	–	9.15	0.03	S>US	–	N/S
(ii) *G*-statistic	Father effect (d.f. = 1)			Handling effect (d.f. = 1)			4 Groups (d.f. = 3)	
Variable	*G*-statistic	*P*-value	Direction	*G*-statistic	*P*-value	Direction	*G*-statistic	*P*-value
Hiss	4.82	0.05	F<UF	–	N/S	–	–	N/S
Growl	–	N/S	–	3.0	0.1	S<US	5.9	0.1
Flat posture	7.14	0.05	F<UF	4.55	0.05	S<US	9.63	0.05
Hiding	5.84	0.05	F<UF	–	N/S	–	7.64	0.1
Purr	–	N/S	–	–	N/S	–	–	N/S
Arch back	5.06	0.05	F>UF	9.45	0.0	S>US	11.18	0.05
Knead paws	–	N/S	–	–	N/S	–	–	N/S
Tail up	3.5	0.1	F>UF	5.17	0.05	S>US	–	N/S
Body roll	–	N/S	–	–	N/S	–	–	N/S
Rub person	–	N/S	–	–	N/S	–	–	N/S

[a] $n = 12$ (litter means), otherwise $n = 37$ (individual means). N/S, $P > 0.1$.

Table 4
Novel Box Test: effects of father's friendliness and early handling experience (ANOVA)

	Father effect (d.f. = 1)			Handling effect (d.f. = 1)			Interaction	
Variable	*F*-value	*P*-value	Direction	*F*-value	*P*-value	Direction	*F*-value	*P*-value
Latency to emergence[a]	7.08	0.05	F<UF	7.94	0.03	S<US	–	N/S
Latency to 1 m	14.83	0.0	F<UF	–	N/S	–	–	N/S
Latency to 50 cm[a]	10.08	0.03	F<UF	–	N/S	–	–	N/S
Latency to touch[a]	19.49	0.01	F<UF	–	N/S	–	–	N/S
Latency to rub[a]	–	N/S	–	–	N/S	–	–	N/S
No. of rubs[a]	–	N/S	–	–	N/S	–	–	N/S
No. of times in box[a]	15.3	0.01	F>UF	–	N/S	–	–	N/S
Part body in box[a]	15.93	0.01	F<UF	–	N/S	–	–	N/S
Whole body in box[a]	15.77	0.01	F<UF	–	N/S	–	–	N/S
Total time in box[a]	4.27	0.1	F>UF	–	N/S	–	–	N/S
Total time < 1 m[a]	18.38	0.01	F>UF	–	N/S	–	–	N/S
No. of vocals[a]	–	N/S	–	5.11	0.01	S>US	–	N/S

[a] $n = 12$ (litter means), otherwise $n = 37$ (individual means). N/S, $P > 0.1$.

greeting ritual. Socialised cats were less likely than unsocialised cats to adopt a flattened posture; a form of defensive behaviour. They were also more likely to show relaxed behaviour: arch their back and raise their tail.

Interactions between the two effects were significant for flattened posture and arch back (Table 3). Pairwise analyses of differences between the four treatment groups revealed friendly-fathered socialised (F/S) cats accounted for most of the deviation from a random distribution of data (Fig. 5). They were less likely than other groups to adopt a flattened posture ($G = 7.60$, d.f. $= 1$, $P < 0.01$) and were more likely than other groups to arch their back ($G = 10.65$, d.f. $= 1$, $P < 0.005$).

The Novel Box results (Table 4) showed that a cat's early handling experience was not important in determining how it later responded to a novel object. Socialised and unsocialised cats were equally distressed when faced with a novel object. However, cats from 'friendly' fathers and 'unfriendly' fathers clearly differed in their response to the novel box. Friendly-fathered cats were quicker to approach, touch and enter the box, they entered the box more often and stayed close to the box for longer than the unfriendly-fathered cats (Table 4). Both friendly-fathered cats and socialised cats were quicker to emerge from their carry basket when placed in the test room. Friendly-fathered cats were less likely to hide during the test ($G = 5.46$, $P < 0.05$). No significant interactions were found.

4. Discussion

The general result from previous studies is clear; early handling produces cats that are friendlier to people. The results in this study confirm that early handling produces significant differences between cats in their response to a familiar person. Cats socialised as kittens are friendlier to a test person than cats unsocialised as kittens. Genetic variation also produced significant differences between cats in their response to a familiar person. Cats fathered by a 'friendly' father were friendlier to the person than cats from an 'unfriendly' father. These results agree with Turner et al.'s study (1986) which found that kittens could be differentiated by their father's temperament.

Maternal effects on friendliness may also be operating, but as kittens are raised with their mother, maternal effects could arise from both genetic and experiential sources. As I wanted to look specifically at genetic effects I only considered father effects in this study. Fält (1984) found a maternal effect, in addition to an effect of paternity, on her puppies' behaviour. Likewise Turner et al. (1986) found both effects of paternity and maternity on offspring behaviour at their study site in Zurich, although only effects of paternity at the Cambridge site. They explained the difference by the closer relatedness of the Cambridge mothers (hence less genetic variability) relative to the Swiss mothers.

Unsocialised cats and unfriendly-fathered cats were more likely to hiss at the test person, to adopt a flattened posture and to hide. All these behaviour patterns are associated with distressed or threatened cats (Collard, 1967; Adamec et al., 1983; Dards, 1983: Guyot et al., 1983; McCune, 1992). In contrast, friendly-fathered cats were more likely to raise their tail, arch their back, knead their paws, rub the test person and body roll, behaviour associated with sociable, relaxed cats (Moelk, 1944, 1979; Fox, 1975: Leyhausen, 1979; Mertens, 1991; Turner, 1991). In cats, all these behaviour patterns are associated with lack of distress.

The four treatment groups in this study combined the two manipulated variables: father's friendliness and early handling experience. In the home pens, the personality or behavioural style (after Mendl and Harcourt, 1988) of cats in the four groups seemed to fall into three basic types: (1) very friendly (F/S); (2) intermediate friendliness (F/US and UF/S (indistinguishable)); (3) very unfriendly (UF/US).

Statistical distribution of test data within the four treatment groups did not always fall into three corresponding groups. For most tests, friendly-fathered socialised (F/S) cats accounted for most of the deviation from a random distribution of data. For these variables, the data fell into two groups: friendly-fathered socialised cats and the rest, which were indistinguishable from each other. However, the distribution did differ according to the particular variable. For example, data for the variable 'Hiss' in the familiar person approach test (FAT) fell into three groups: friendly-fathered, socialised cats (F/S), unfriendly-fathered, unsocialised cats (UF/US), and then both friendly-fathered, unsocialised cats (F/US), and unfriendly-fathered, socialised cats (UF/S) which were indistinguishable from each other.

The stranger approach tests (SAT) showed these differences in friendliness were not limited to the person who had conducted the early handling but extended to other people. Few of the significant results which differentiated cats according to handling experience or friendliness of father in the FAT were lost in the SAT. However there was a general inhibition of response in the SAT compared to the FAT reducing the differences between socialised and unsocialised cats which might be explained by the testing context of the SAT posing a greater threat to the cats than the FAT.

One of the ways in which cats respond to threat is by behavioural inhibition (Michael, 1961; Meier, 1968; Konrad and Bagshaw, 1970; Adamec and Stark-Adamec; 1989. Carlstead et al., 1993; McCune, 1992). If the SAT posed a greater threat to the cats than the FAT, as is intuitively assumed, then greater inhibition would be expected in the SAT compared with the FAT. Longer latency values for cats, from the same father and with the same early handling experience, in the SAT compared with the FAT, indicate greater behavioural inhibition in the second test.

The third experiment, the Novel Box test, was designed to tease apart the response of cats to novel objects that are people and to novel objects in general. The handling effect could be hypothesised as determining stress sensitivity in some way which would influence the response of cats to all novel objects. The genetic contribution to friendliness might work in a similar way, perhaps facilitating the socialisation process by reducing fear. Certainly F/S kittens were noticeably less fearful of their handler during the handling sessions during their early socialisation period compared with the UF/S kittens. For example, F/S kittens were the only kittens to climb onto the handler's shoulders and to purr when being stroked. As both F/S and UF/S kittens received the same treatment, the difference between them can be attributed to their father's friendliness. In this way both effects could possibly produce differences in cats' responses to novelty. Evidence from studies of other species indicate that early experience can have profound effects on an individual's response to novelty or stress (Seitz, 1959; Konrad and Bagshaw, 1970; Guyot et al., 1983; Pedersen and Jeppesen, 1990).

Neither of the predictions posed in the Introduction were observed. Results from the Novel Box test did not follow the pattern of the FAT and SAT. Cats could be differentiated

Table 5
Summary of common cat personality types (after Karsh and Turner, 1988)

(i)	Feaver et al.'s 'sociable, confident, easy-going'. Karsh's 'confident' and Meier and Turner's (1985) 'trusting'
(ii)	Feaver et al.'s 'timid, nervous', Karsh's 'timid' and Turner's 'shy' and 'unfriendly'
(iii)	Feaver et al.'s 'active, aggressive' and Karsh's 'active' analogous to Pavlov's excitatory temperament

in their response to a novel object according to the friendliness of their father but not according to their early handling experience. If the response of cats to people is simply part of a wider response to novelty, both the father effect and the handling effect would be expected to differentiate between cats in their response to the novel box. It is not that 'friendliness' is making a difference to the cat's response but that specifically the genetic contribution to friendliness is making the difference.

The Novel Box results indicated that 'friendliness' of father may be associated with some other characteristic. Indeed, if definitions of 'friendliness' used by other authors are examined, they all contain an element equivalent to boldness (Table 5). Type one personality includes elements of boldness (i.e. confident) as well as friendliness (sociable, which includes lack of hostility to people, lack of being tense and lack of fear components. Feaver et al., 1986). Can the boldness element in these descriptions of friendliness in some way be attributed to the father effect? Differences due to the handling effect disappeared in the Novel Box test when no one was present during the test, implying that the handling effect might be restricted to a perception of people. Similarly, as cats could be differentiated in this test according to the friendliness of their father, it seemed that the genetic effect may indeed be a general effect that could be termed boldness.

This conclusion, that the handling effect is specific to people and that the genetic effect is a general response, was checked by further analysis of differences between treatment groups. In tests with a person present, treatment groups can be compared for both the Father effect (general) and the Handling effect (specific). Thus the F/US and UF/S groups should be indistinguishable as both groups have one factor shown to promote friendliness (***F***/US and UF/***S***) and one factor against (F/***US*** and ***UF***/S). In tests without a person present (the Novel Box test), treatment groups can be compared for only one effect, the Father effect because the Handling effect cannot be elicited. Thus, F/US and UF/S groups should be distinguishable because the measurable effect is different in each group (***F***/US and ***UF***/S).

Analysis of the data supported these predictions. Using Mann–Whitney tests, F/US and UF/S data were indistinguishable for all FAT and SAT measures (person present during testing). But in the Novel Box test, data from F/US and UF/S groups could be distinguished for two measures: (1) latency to approach within 1 m ($U=20, P<0.05$) where F/US cats were quicker to approach than UF/S cats and (2) total time spent within 1 m (trend only, $U=21.5, P<0.10$) where F/US cats stayed for longer than UF/S cats. When these two groups were compared with the other treatment groups, the F/S and F/US groups were found to be indistinguishable, which would be expected in a test with no person present to elicit differences due to Handling (i.e. no difference in ***F***/S vs. ***F***/US). Likewise, UF/S cats were indistinguishable from UF/US cats as expected (i.e. no difference in ***UF***/S vs. ***UF***/US).

These results do not support those of Wilson et al.'s (1965) study where a handling effect differentiated kittens in their response to a novel toy. The kittens were tested each day for 5 days, thus they may have become habituated to the toys in that period (Konrad and Bagshaw, 1970) because, unlike people, the toys were predictable and unmoving. Perception of the toys may have changed from the toys posing a threat to one of interest, eliciting exploratory behaviour. As my tests were only conducted twice for each cat, the testing period was likely to have been too short to enable sufficient habituation to the novel object.

To summarise, as differences between cats according to socialisation experience disappeared in the Novel Box test, when no person was present, the interpretation is that the Handling effect specifically relates to the cat's perception of people. As cats could be differentiated in this test according to the friendliness of their father, the genetic contribution to friendliness seems to be a general effect that is not restricted to these cats' perception of people but extends to other novel objects.

In addition to being friendlier to people, friendly-fathered cats and socialised cats also coped better when faced with the challenge of meeting a stranger, something cats must regularly face, for example when visiting the vet, being boarded in a cattery or being handled in an experiment. Their welfare was better than unfriendly-fathered cats and unsocialised cats because, when faced with a stranger, they were less likely to show behaviour associated with distress and more likely to show behaviour associated with being relaxed.

'Friendliness' is highly desired by cat owners and has beneficial consequences for cat welfare. Consequently, consideration of appropriate breeding and rearing strategies should enable cats to be raised that are better able to meet the challenge of living alongside people.

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