

Evidence suggesting preadaptation to domestication throughout the small Felidae

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One obstacle in the development of a coherent theoretical framework for the process of animal domestication is the rarity of domestication events in human history. It is unclear whether: (1) many species are suitable for domestication, the limiting factor being the requirement of people for new domestic animals; or (2) very few species are preadapted for domestication. Comparisons between 16 species and subspecies of small cats (Felidae) kept in zoos indicated that affiliative behaviour towards people, an important preadaptation to domestication, is widely, if patchily, distributed throughout this taxon, and is not concentrated in species closely related to the domestic cat, *Felis silvestris catus*. The highest proportion of individuals showing affiliative behaviour was found in the ocelot lineage, which is estimated to have diverged from the rest of the Felidae between 5 and 13 Mya. The domestication of *F. silvestris* alone among felids is therefore likely to have been the result of a specific set of human cultural events and requirements in the Egyptian New Kingdom, rather than the consequence of a unique tendency to tameness in this subspecies. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 75, 2002, 361–366.

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INTRODUCTION

The study of the domestication process can provide information for at least three other areas of biological science. It can act as a model for evolutionary processes (Haldane, 1954), particularly those that are driven by environmental stress (Kohane & Parsons, 1988), although this approach is less fashionable than it was in the first half of the twentieth century (Lickliter & Ness, 1990). In animal welfare science, it is essential to understand to what extent the decision rules of the ancestral species have been altered by domestication, as negative subjective experiences ('suffering') are most likely to result from a mismatch between an animal's current environment and the environment in which its decision rules evolved (Barnard & Hurst, 1996). An understanding of domestication is also important to conservation biology. The reintroduction of endangered species bred in captivity is more likely to be successful if the process of domestication has not accidentally started during captive

breeding, for which greater understanding of the earliest stages of this process is needed (Price, 1984). An alternative view, that domestication is a possible means of saving species from extinction, has recently been proposed by Archer & Pain (2000).

The phenotypic differences between domesticated and undomesticated versions of a species are usually ascribed to genetic changes occurring during domestication. These include natural selection, genetic drift and mutation, as well as artificial selection, the consequences of inbreeding (Price & King, 1968), and the effects of the domestic environment on behavioural ontogeny (Boice, 1981; Clark & Galef, 1981). In contrast to plants, of which hundreds of species have been domesticated (Hawksworth & Kalin-Arroyo, 1995), domestications of animals appear to be rare. Less than ten species have been fully domesticated (Clutton-Brock, 1987), although in two, cattle (Loftus *et al.*, 1994) and dogs (Vilà *et al.*, 1997), mtDNA evidence has pointed to at least two distinct domestication events. There are at least two possible causes for this rarity: (1) many species are suitable for domestication, and the limitation has been the requirement of people for domesticated animals, or (2) very few species are

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preadapted (more correctly, exapted, Gould & Vrba, 1982) for domestication. Distinguishing between these two possibilities, however, is not straightforward, as in a successful domestication, biological and cultural processes have to run in parallel (Clutton-Brock, 1992). Concentration of preadaptation in discrete taxa is supported by the over-representation of two Orders of vertebrates among the main domesticated species: Artiodactyla, in particular the Family Bovidae, and Galliformes (Hale, 1969). This suggests that many wild species within these groups were preadapted to domestication, and implies that other Orders might contain a lower proportion of preadapted species.

The 'domestic' cat, *Felis silvestris catus*, the only domesticated member of its Family (Clutton-Brock, 1987), is usually classified as partially, rather than fully, domesticated (Bradshaw *et al.*, 1999). The criteria for complete domestication, permanent isolation from the wild species, and human control of breeding, territory and food supply (Clutton-Brock, 1992), are satisfied by pedigree breeds such as Persian and Siamese. None of these, however, apply to all populations of non-pedigree or 'mongrel' cats, which hybridize with wild *F. silvestris* (Daniels *et al.*, 1998), select their own mates and compete for territories (Liberg *et al.*, 2000), and retain the ability to hunt and scavenge for food (Fitzgerald & Turner, 2000). The ancestral subspecies *F. s. libyca* (Randi & Ragni, 1991) fulfils only approximately half of the criteria for preadaptation to domestication proposed by Hale (1969). Specifically, its domestication should have been impeded for the following reasons: it is territorial and does not form large cohesive social groups with a permanent hierarchy (Macdonald, Yamaguchi & Kerby, 2000); in much of its range it is generally wary of man (Smithers, 1983; Happold, 1987); it has specialized dietary requirements (Bradshaw *et al.*, 1996); and it is extremely agile. This apparently low level of preadaptation suggests that human needs in the Egyptian New Kingdom must have been the primary factor that initiated the domestication of the cat over 3500 years ago. We have attempted to test this hypothesis by examining whether other members of the Felidae are at least as preadapted as *F. silvestris* is. If so, a specific human need, combined with the availability of *F. s. libyca* in north-east Africa, rather than any special biological characteristics, is likely to have been the primary driver of the domestication of this species.

If biological characteristics are important, then by analogy with the examples from the Bovidae and Galliformes cited above, species within the domestic cat lineage should be more preadapted than species in the other felid lineages. The phylogeny of the Felidae is currently under some dispute, but most authors

support three major clades, the *Panthera* group, the ocelot lineage, and the domestic cat lineage (Bininda-Emonds, Gittleman & Purvis, 1999), although the precise composition of the domestic cat group, which is important for our hypothesis, varies slightly between authors (compare Collier & O'Brien, 1985; Johnson & O'Brien, 1997; Bininda-Emonds *et al.*, 1999; Mattern & McLennan, 2000). In this paper we have used the scheme of Bininda-Emonds *et al.* (1999), that combines data from a wide variety of sources.

We have concentrated on probably the most important single preadaptation accessible to measurement, the extent to which members of a species become tame when kept in captivity, i.e. an 'inborn liking for man' (Clutton-Brock, 1987). Anecdotally, this is considered to be very variable within the Felidae.

METHODS

Questionnaires were used to obtain information from zookeepers about the affiliative behaviour directed towards them by individual members of the Felidae. This method of collecting data concerning captive animals has been shown to be reliable by Carlstead (1997). In each case, species, subspecies or race, age, sex, whether hand- or mother-reared, and the occurrence of four types of behaviour were recorded. These types of behaviour were: sitting within 1 m of the keeper; rolling within 1 m of the keeper; head or flank rubbing on the keeper; and licking the keeper.

Information was only requested for species of the size of a lynx or smaller. This was because the size of the larger species was thought likely to affect the behaviour of their keepers, and the larger species ('big cats') seem unlikely to be direct competitors of *F. silvestris libyca* for domestication. Questionnaires were returned from 71 zoos in the USA, UK and Republic of South Africa, providing information on 22 species, and three subspecies of *Felis silvestris* (*silvestris*, *libyca* and *ornata*) which were kept separate as *catus* is also a subspecies of *F. silvestris* (Randi & Ragni, 1991). For simplicity, these subspecies will subsequently be referred to as 'species'. Individual cats whose keeper did not enter their cages while they were unrestrained were excluded from further analysis, which was then confined to the 16 remaining species represented by five or more individuals (Table 1).

For each species, the following parameters were calculated: the proportion of individuals within a species whose keepers entered their cages; the proportion of individuals within each species that had ever showed any of the four types of affiliative behaviour towards their keepers. The proportion of individuals within each species ever showing tactile affiliative behaviour towards their keepers, i.e. rubbing and or licking, were

Table 1 Interactions between small cats of 16 species/subspecies kept in zoos and their keepers, arranged by their lineage within the family Felidae (Bininda-Emonds *et al.*, 1999; Mattern & McLennan, 2000)

Lineage/species	Keepers in ^a	N ^b	Proportion affiliative ^c	Proportion rub/lick ^d	Tactile behaviour ^e	
					Rub	Lick
Domestic cat lineage						
<i>Felis silvestris libyca</i>	1.00	12	0.83	0.17	2	2
<i>Felis silvestris ornata</i>	1.00	12	0.25	0.08	1	0
<i>Felis silvestris silvestris</i>	1.00	14	0.14	0.00	0	0
<i>Felis chaus</i>	1.00	17	0.41	0.06	1	1
<i>Felis margarita</i>	0.75	6	0.67	0.00	0	0
Domestic cat/caracal lineage						
<i>Caracal caracal</i>	0.70	21	0.29	0.14	1	2
<i>Leptailurus serval</i>	0.65	15	0.33	0.07	1	1
Asian leopard cat group						
<i>Prionailurus rubiginosus</i>	1.00	5	0.20	0.00	0	0
<i>Prionailurus viverrinus</i>	0.67	14	0.21	0.07	1	0
<i>Prionailurus bengalensis</i>	1.00	16	0.00	0.00	0	0
Lynx group						
<i>Lynx rufus</i>	0.86	24	0.21	0.08	2	1
<i>Lynx lynx</i>	0.84	32	0.50	0.03	1	0
<i>Lynx canadensis</i>	1.00	29	0.07	0.00	0	0
Ocelot lineage						
<i>Oncifelis geoffroyi</i>	1.00	6	0.83	0.33	2	2
<i>Leopardus pardalis</i>	0.81	29	0.52	0.17	4	5
<i>Leopardus wiedii</i>	0.85	11	0.91	0.18	2	0

^a Keepers in, proportion of individuals within a species whose keepers went into their cages.
^b Sample size for proportion affiliative and rub/lick; includes only mother-raised cats whose keepers entered their cages.
^c Proportion affiliative, proportion of individuals within each species that had ever showed any affiliative behaviour towards their keepers.
^d Proportion rub/lick, the proportion of individuals within each species that ever rubbed on and/or licked their keepers.
^e Tactile behaviour, the number of individual cats that had ever displayed rub and lick towards their keepers.

also calculated, as these are characteristic of domesticated animals such as the domestic cat and domestic dog. An estimate of the average size of each species was calculated from means of the combined head and body lengths, weighted by sample size if given, in Tables A.1–A.3 of Kitchener (1991).

For analysis, species were grouped according to the clades in Bininda-Emonds *et al.* (1999). The caracal and the serval were initially included in the domestic cat lineage. When significant differences between lineages were found, the analysis was repeated with these two species in a separate group, as supported by Mattern & McLennan (2000).

each species, represented by five or more individuals ($N = 17$), the proportion of individuals whose cages keepers entered (Table 1) was uncorrelated with size (Spearman rank correlation coefficient $\chi = 0.233$, $P = 0.37$), and was unaffected by lineage (one way ANOVA on ranked proportions, $F = 0.80$, d.f. = 3, $P = 0.97$). In addition to the species in Table 1, *Felis nigripes* (domestic cat lineage) was included in this analysis but not in subsequent analyses as the sample size dropped to below five when individuals whose keepers did not enter their cages were excluded.

RESULTS

KEEPER BEHAVIOUR

We first checked whether opportunities for affiliative behaviour were affected by keeper behaviour. Within

HAND-REARING

Social behaviour is markedly affected in felids raised from birth by humans (Mellen, 1988). The 31 hand-reared individuals were far more likely to show affiliative behaviour of any kind, compared with the 263

mother-reared ($\chi^2 = 26.6$, d.f. = 1, $P < 0.001$), and were excluded from further analysis.

DIFFERENCES BETWEEN SPECIES AND LINEAGES

The proportion of mother-raised individuals within each species showing any affiliative behaviour (Table 1) was compared with the median age of each species sample, in the event of young, potentially more sociable, individuals being over-represented in some species. This was not significant (Spearman rank correlation coefficient $\chi = 0.174$, $P = 0.52$). To exclude the possibility of keepers being more wary of larger species, the proportion showing affiliative behaviour was also compared with size; this was also non-significant ($\chi = -0.139$, $P = 0.62$). Comparisons between species and lineages should therefore reflect species-specific differences in tendencies towards tameness.

The three species from the ocelot lineage were among the five species ranked as containing the most individuals showing affiliative behaviour. On average, species in this lineage were significantly more affiliative than the species from the lynx or leopard cat groups, with the domestic cat lineage intermediate (one-way ANOVA on ranked proportions; $F = 5.01$, d.f. = 3,12; $P = 0.02$; Waller-Duncan multiple-range test at Seriousness Ratio = 100). Separation of the caracal group from the domestic cat lineage had little effect on this analysis ($F = 3.50$; d.f. = 4,11; $P = 0.05$). Outside the ocelot lineage, the most affiliative species was *F. s. libyca*, the ancestor of *F. s. catus*. The sample of *libyca* ($N = 12$) had mainly originated in Arabia (race *F. s. tristrami*); neither of the two individuals originating from southern Africa exhibited any affiliative behaviour.

Only a small number (21) of individual cats were reported to have shown tactile behaviour (head- or flank-rubbing, licking) towards their keepers. Licking was slightly less common than rubbing (Table 1), and usually occurred in individuals which also rubbed; the exceptions were two *Caracal caracal* and one *Leopardus pardalis*. The distribution of tactile behaviour between species broadly followed the same pattern as general affiliative behaviour (Table 1). The species with the highest proportions were *Oncifelis geoffroyi*, *Leopardus weidii*, *L. pardalis* (all ocelot lineage), *F. s. libyca*, and *Caracal caracal*. The ocelot lineage contained significantly more tactile individuals than any of the other three lineages which were not significantly different from one another (one-way ANOVA on ranked proportions; $F = 4.63$, d.f. = 3,12; $P = 0.02$; Waller-Duncan multiple range test at Seriousness Ratio = 100). When the analysis was repeated with the caracal lineage separated from the domestic cat lineage, the ocelot lineage was significantly separated from the domestic, lynx and leopard

cat lineages but not from the caracal lineage ($F = 3.62$, d.f. = 4,11; $P = 0.04$). At least one individual, however, from each lineage performed rubbing; licking was reported from all lineages except the Asian leopard cat group.

DISCUSSION

We have found that the expression of affiliative behaviour towards people is not concentrated in the close relatives of the domestic cat, but is widely, if patchily, distributed throughout the Felidae. The four types of affiliative behaviour, including tactile behaviour such as body-rubbing and licking, are also well-distributed among the three lineages. A similarly wide distribution of reproductive and other behaviour patterns across the Felidae, which in general appear to share many aspects of their behavioural repertoire, was reported by Mellen (1993).

The sample of the ancestral subspecies for the domestic cat, *F. s. libyca*, included a high proportion of affiliative individuals, two of which rubbed and licked their keepers. This may be an underestimate, as the sample may not have included examples of the most tameable races; anecdotal evidence suggests that in some parts of its range, not represented in our sample, this subspecies may be easy to tame (Smithers, 1968; Guggisberg, 1975). The two human-friendly individuals classified as *F. silvestris silvestris* may have been hybrids with *catus* having wild-type pelage (Daniels *et al.*, 1998).

Several other species, in particular Geoffroy's cat *Oncifelis geoffroyi*, the margay *Leopardus weidii*, and the sand cat *F. margarita*, also had a high proportion of individuals which displayed affiliative behaviour towards their keepers, although *F. margarita* was represented by only six individuals, which may not have been representative. All three representatives of the ocelot lineage, and also the caracal, had several individuals that rubbed and/or licked their keepers. Depending upon how crucial physical contact, as opposed to tolerance of proximity to man, is to the ease of domestication, any or all of the above mentioned species may be preadapted for domestication. None are particularly closely related to *F. s. libyca*. The ancestral species of the ocelot lineage diverged from the other Felidae ~16 Mya (Bininda-Emonds *et al.*, 1999), and both the margay and Geoffroy's cat, may be more closely related to the lynx group than to the domestic cat (Bininda-Emonds *et al.*, 1999). The sand cat, although a member of the domestic cat lineage, probably diverged ~2.3 Mya (Bininda-Emonds *et al.*, 1999), and both *F. s. silvestris* and *F. s. ornata*, with lower proportions of friendly individuals than *margarita*, are more closely related to *catus*. The caracal may not be particularly closely related to any of the

other members of the Felidae (Bininda-Emonds *et al.*, 1999). A tendency towards tameness is therefore unlikely to account for the single domestication within the Felidae, and alternative explanations need to be investigated.

The ocelot lineage is confined to South America. The guinea pig, llama and alpaca were probably first domesticated on this continent (Hale, 1969), and attempts were made to domesticate the local foxes *Dusicyon* spp. (Clutton-Brock, 1977): this suggests that there should have been no conceptual barrier to the domestication of another carnivore. The sand cat is found in desert and semi-desert habitats in Africa and Asia, and may therefore have had little opportunity to interact with human settlements. The caracal, by contrast, is found in a wide range of habitats throughout Africa, Arabia, south-western Asia and India, and has been tamed successfully (Kitchener, 1991); its large size (~12 kg) may make it less suitable for domestication than the smaller *F. s. lybica* (~4 kg). Ecological and geographical separation between man and potential domesticants may therefore explain why some species were not domesticated, but is unlikely to have been a significant barrier for several others.

One such is the jungle cat *F. chaus*, specimens of which were mummified by the Egyptians in the first millennium BC (Morrison-Scott, 1952); there has been speculation that this species was domesticated in Egypt and also in India (Clutton-Brock, 1987). The reporting of seven individuals which were human-friendly, one of which rubbed against and licked its keeper, suggests that the domestication of this species may be relatively easy. Recently, hybridization between *F. chaus* and *F. catus* has been used to develop the Chausie breed (Helgren, 1997). Conversely, the successful domestication of another hybrid, the Bengal cat, originally derived from crosses between domestic cats and *P. bengalensis* (Helgren, 1997), would not be predicted from the complete absence in our sample of affiliative behaviour by *P. bengalensis* towards keepers.

The single domestication event within the Felidae, apart from these modern hybrids, might suggest that this group is behaviourally poorly preadapted for domestication. This study, however, suggests that this is not the case. Overall, the distribution of the tendency to tameness among the small felids points to a localized human need as being the primary reason for the domestication of *F. s. lybica*, rather than any special features of its behavioural biology.

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REFERENCES

- Archer M, Pain S. 2000.** Opinion interview: my pet possum. *New Scientist* **166** (2236): 40–43.
- Barnard CJ, Hurst JL. 1996.** Welfare by design: the natural selection of welfare criteria. *Animal Welfare* **5**: 405–433.
- Bininda-Emonds ORP, Gittleman JL, Purvis A. 1999.** Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biological Reviews* **74**: 143–175.
- Boice R. 1981.** Captivity and feralisation. *Psychological Bulletin* **89**: 407–421.
- Bradshaw JWS, Goodwin D, Legrand-Defréin V, Nott HMR. 1996.** Food selection by the domestic cat, an obligate carnivore. *Comparative Biochemistry and Physiology* **114A**: 205–209.
- Bradshaw JWS, Horsfield GF, Allen JA, Robinson IH. 1999.** Feral cats: their role in the population dynamics of *Felis catus*. *Applied Animal Behaviour Science* **65**: 273–283.
- Carlstead K. 1997.** The reliability and validity of keeper ratings of animal behaviour as a method for evaluating the husbandry of endangered species in zoos. In: Hemsworth PH, Špinka M, Košťál L, eds. *Proceedings of the 31st International Congress of ISAE*. Prague: Research Institute of Animal Production, 62.
- Clark MM, Galef BG. 1981.** Environmental influence on development, behavior, and endocrine morphology of gerbils. *Physiology and Behaviour* **27**: 761–765.
- Clutton-Brock J. 1977.** Man-made dogs. *Science* **197**: 1340–1342.
- Clutton-Brock J. 1987.** *A natural history of domesticated animals*. Cambridge/London: Cambridge University Press/British Museum of Natural History.
- Clutton-Brock J. 1992.** The process of domestication. *Mammal Review* **22**: 79–85.
- Collier GE, O'Brien SJ. 1985.** A molecular phylogeny of the Felidae – immunological distance. *Evolution* **39**: 473–487.
- Daniels MJ, Balharry D, Hirst D, Kitchener AC, Aspinall RJ. 1998.** Morphological and pelage characteristics of wild living cats in Scotland: implications for defining the 'wildcat'. *Journal of Zoology* **244**: 231–247.
- Fitzgerald BM, Turner DC. 2000.** Hunting behaviour of domestic cats and their impact on prey populations. In: Turner DC, Bateson P, eds. *The domestic cat: the biology of its behaviour*, 2nd edn. Cambridge: Cambridge University Press, 151–175.
- Gould SJ, Vrba ES. 1982.** Exaptation – a missing term in the science of form. *Paleobiology* **8**: 4–15.
- Guggisberg CAW. 1975.** *Wild cats of the world*. London: David & Charles, 32–35.
- Haldane JBS. 1954.** The statics of evolution. In: Huxley J, Hardy AC, Ford EB, eds. *Evolution as a process*. London: Allen & Unwin, 109–121.

- Hale EB. 1969.** Domestication and the evolution of behavior. In: Hafez ESE, ed. *The behaviour of domestic animals*. London: Baillière, Tindall & Cassell, 22–42.
- Happold DCD. 1987.** *The mammals of Nigeria*. Oxford: Clarendon Press, 179.
- Hawksworth DL, Kalin-Arroyo MT. 1995.** Magnitude and distribution of biodiversity. In: Heywood VH, ed. *Global biodiversity assessment*. Cambridge: Cambridge University Press, 107–191.
- Helgren JA. 1997.** *Barron's encyclopedia of cat breeds: a complete guide to the domestic cats of North America*. New York: Barrons Educational Series, Inc.
- Johnson WE, O'Brien SJ. 1997.** Phylogenetic reconstruction of the Felidae using 16S rRNA and NADH-5 mitochondrial genes. *Journal of Molecular Evolution* **44** (Suppl. 1): S98–S116.
- Kitchener A. 1991.** *The natural history of the wild cats*. London: Christopher Helm.
- Kohane MJ, Parsons PA. 1988.** Domestication: evolutionary change under stress. *Evolutionary Biology* **23**: 31–48.
- Liberg O, Sandell M, Pontier D, Natoli E. 2000.** Density, spatial organisation and reproductive tactics in the domestic cat and other felids. In: Turner DC, Bateson P, eds. *The domestic cat: the biology of its behaviour*, 2nd edn. Cambridge: Cambridge University Press, 83–98.
- Lickliter R, Ness JW. 1990.** Domestication and comparative psychology: status and strategy. *Journal of Comparative Psychology* **104**: 211–218.
- Loftus RT, MacHugh DE, Bradley DG, Sharp PM, Cunningham P. 1994.** Evidence for two independent domestications of cattle. *Proceedings of the National Academy of Sciences* **91**: 2757–2761.
- Macdonald DW, Yamaguchi N, Kerby G. 2000.** Group-living in the domestic cat: its sociobiology and epidemiology. In: Turner DC, Bateson P, eds. *The domestic cat: the biology of its behaviour*, 2nd edn. Cambridge: Cambridge University Press, 95–118.
- Mattern MY, McLennan DA. 2000.** Phylogeny and speciation of felids. *Cladistics* **16**: 232–253.
- Mellen JD. 1988.** The effects of hand-raising on sexual behavior of captive small felids using domestic cats as a model. *Annual Proceedings of the American Association of Zoological Parks and Aquariums*. Milwaukee: AAZPA, 253–259.
- Mellen JD. 1993.** A comparative-analysis of scent-marking, social and reproductive behavior in 20 species of small cats (*Felis*). *American Zoologist* **33**: 151–166.
- Morrison-Scott TCS. 1952.** The mummified cats of Ancient Egypt. *Proceedings of the Zoological Society of London* **121**: 861–867.
- Price EO. 1984.** Behavioral aspects of animal domestication. *Quarterly Review of Biology* **59**: 1–32.
- Price EO, King JA. 1968.** Domestication and adaptation. In: Hafez ESE, ed. *Adaptation of domestic animals*. Philadelphia: Lea & Febiger, 34–45.
- Randi E, Ragni B. 1991.** Genetic variability and biochemical systematics of domestic and wild cat populations (*Felis silvestris*: Felidae). *Journal of Mammalogy* **72**: 79–88.
- Smithers RHN. 1968.** Cat of the pharaohs: the African wild cat from past to present. *Animal Kingdom* **61**: 17–23.
- Smithers RHN. 1983.** *The mammals of the southern African subregion*. Pretoria: University of Pretoria, 386–391.
- Vilà C, Savolainen P, Maldonado JE, Amorim IR, Rice JE, Honeycutt RL, Crandall KA, Lundeberg J, Wayne RK. 1997.** Multiple and ancient origins of the domestic dog. *Science* **276**: 1687–1689.