



ORIGINAL ARTICLE

## An insight into population structure and gene flow within pure-bred cats

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### Keywords

Cat; gene flow; genetic variability; inbreeding; population structure.

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### Summary

Investigation of genetic structure on the basis of pedigree information requires indicators adapted to the specific context of the populations studied. On the basis of pedigree-based estimates of diversity, we analysed genetic diversity, mating practices and gene flow among eight cat populations raised in France, five of them being single breeds and three consisting of breed groups with varieties that may interbreed. When computed on the basis of coancestry rate, effective population sizes ranged from 127 to 1406, while the contribution of founders from other breeds ranged from 0.7 to 16.4%. In the five breeds,  $F_{IS}$  ranged between 0.96 and 1.83%, with this result being related to mating practices such as close inbreeding (on average 5% of individuals being inbred within two generations). Within the three groups of varieties studied,  $F_{IT}$  ranged from 1.59 to 3%, while  $\overline{F_{ST}}$  values were estimated between 0.04 and 0.91%, which was linked to various amounts of gene exchanges between subpopulations at the parental level. The results indicate that cat breeds constitute populations submitted to low selection intensity, contrasting with relatively high individual inbreeding level caused by close inbreeding practices.

### Background

Genealogies constitute a profitable source of information to investigate breeding practices, diversity or genetic structure in livestock, and companion and captive animal populations. Based on Mendelian segregation rules, pedigree analysis can be used to follow gene transmission from generation to generation and between subsamples of an entire population, which may be particularly useful for recently created animal breeds.

Cat breeds may constitute an interesting example of recent populations submitted to various gene flow. Indeed, a majority of modern cat breeds has been developed over the past 50 years, on the basis of simple phenotypical variants, with one or several former populations (Lipinski *et al.* 2008). In companion animals, it has been found that some breeding practices

and a suboptimal management of genetic variability, such as popular sire effect, may lead to a dissemination of inherited disorders and an erosion of genetic diversity. A subsequent increase in inbreeding may eventually lead to an increased incidence of some disorders (Leroy & Baumung 2011) and a negative impact on fitness traits (Boakes *et al.* 2007). These issues have been well studied in dogs using pedigree files, with investigations into breeding practices (Leroy & Baumung 2011), the characterization of genetic diversity (Leroy *et al.* 2006; Calboli *et al.* 2008; Shariflou *et al.* 2011) or inbreeding effects (Mäki *et al.* 2001). Cat breeds are, as well as dog populations, threatened by genetic disorders with more than 250 inherited disorders reported by [Online Mendelian Inheritance in Animals (OMIA), [omia.angis.org.au](http://omia.angis.org.au)]. Yet, pedigree investigations have been less frequently conducted within this species (Mucha *et al.* 2011).

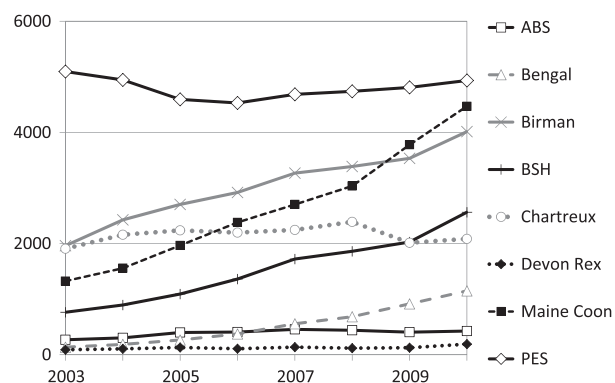
The aim of this study was to analyse the genetic diversity of eight cat pure-bred populations raised in France on the basis of pedigree data. There are two main purposes: (i) to assess the level of genetic variability within cat breeds in relation to inbreeding evolution and specific breeding practices, and (ii) to investigate the recent gene flow explaining current constitution and structure of cat populations.

## Material and methods

### Populations studied

In France, breed genealogies are managed in a unified genealogical database handled by the Livre Officiel des Origines Françaises (LOOF). Among the 66 breeds and varieties registered in France, five breeds and three groups of breeds/varieties were chosen, showing both relatively good pedigree knowledge and a variation in population size or geographical origin. The five breeds are Maine Coon, Bengal, Birman, Chartreux and Devon Rex. Maine Coon and Bengal breeds have experienced a large population increase over the last 8 years (Figure 1): births increasing from 1325 to 4470 and from 136 to 1148, respectively, between 2003 and 2010. Birman and Chartreux breeds, the only two populations of French origin among those studied, have a relatively large number of births (4015 and 2085 registrations in 2010, respectively). By contrast, the Devon Rex breed was considered here as an example of a breed with a small population size (only 191 births in 2010).

The three groups include nine populations, which can be considered as either breeds or varieties depending on countries and the breeding rules of the associations. For more clarity, subpopulations among groups will be considered here as varieties.



**Figure 1** Evolution of births according to breeds over the 2003–2008 period.

The first group (PES) involved two varieties: Persian and Exotic Shorthair. The Persian is one of the most common breeds in the world and until 2010 showed the largest number of births among breeds raised in France (among PES kitties born in 2010, 4934 were registered including 4209 declared as Persian). Cross-breeding is allowed with its shorthaired variety, the Exotic Shorthair breed (725 registrations for 2010). PES is also the only population among those analysed with a decrease in number of births (–13%) between 2003 and 2010 (Figure 1, Table 1). The second group (BSH) involved five varieties (outcrossing being allowed between these populations in France): British Shorthair (1492 births in 2010), its longhair phenotypical variant (295 births), the Scottish variety (504 births), the Highland variety (Scottish longhair variant, 133 births) and the Selkirk variety (140 births). Finally, the Abyssinian population (288 births in 2010) and its long haired Somali variety (139 births in 2010) were also analysed together (ABS).

For each breed or group of varieties, current generation was defined based on individuals registered between 2008 and 2010 with both parents known.

### Methods

We computed the number of equivalent complete generations traced (*EqG*) and generation intervals as described in Leroy *et al.* (2006). Identity-by-descent (*IBD*) estimators, that is, coefficients of inbreeding *F* and coancestry *C*, were computed and averaged over the current generations. To characterize genetic structure within breeds and varieties, we computed fixation index *F<sub>IS</sub>* using the following equation (Leroy &

**Table 1** Demographic parameters of the breeds studied

Breed or group of varieties	Evolution of births (2003–2010) %	Reference population (individuals registered with both parents known over 2008–2010)			
		Nb of breeders	Nb of individuals	Nb of sires	Nb of dams
Abyssinian/Somali (ABS)	+61	115	1 307	163	297
Bengal	+781	241	2896	367	645
Birman	+86	1076	11 109	1087	2352
British Shorthair/British Longhair/Highland/Scottish/Selkirk (BSH)	+198	452	6758	809	1401
Chartreux	+6	514	6494	477	1052
Devon Rex	+96	42	469	82	128
Maine Coon	+225	690	11 642	1215	2178
Persian/Exotic Shorthair (PES)	–13	1300	14 921	2201	3812

Baumung 2011),

$$F_{IS} = \frac{F - C}{1 - C}.$$

For each group (AbS, BSH and PES), we differentiated  $\tilde{F}$  and  $\tilde{C}$  averaged within all varieties, and  $\bar{C}$  as coancestry averaged over the entire group (Caballero & Toro 2002), in order to compute  $F$ -statistics, using the following equations,

$$\overline{F_{IS}} = \frac{\tilde{F} - \tilde{C}}{1 - \tilde{C}}, \overline{F_{ST}} = \frac{\tilde{C} - \bar{C}}{1 - \bar{C}}, F_{IT} = \frac{\tilde{F} - \bar{C}}{1 - \bar{C}},$$

The effective population size was estimated on the basis of individual rates of inbreeding  $\Delta F_i$  and coancestry  $\Delta C_{ij}$  (Cervantes *et al.* 2011), considering  $F_i$  is the inbreeding coefficient of individual  $i$ ,  $C_{ij}$  the coancestry coefficient between individuals  $i$  and  $j$ , and  $EqG_i$  and  $EqG_j$  their respective equivalent complete traced generations:

$$\Delta F_i = 1 - \sqrt[EqG_i]{1 - F_i} \text{ and} \\ \Delta C_{ij} = 1 - \sqrt[EqG_i + EqG_j]{1 - C_{ij}}.$$

Effective population sizes were estimated by averaging  $\Delta F_i$  over the current generation and  $\Delta C_{ij}$  over 100 000 pairs of individuals randomly sampled among the current generation, using the following formulas:

$$N_{eFi} = 1/2\overline{\Delta F} \text{ and } N_{eCi} = 1/2\overline{\Delta C}.$$

Percentages of inbred individuals were computed using the Van Raden (1992) method taking into account only two and three generations. The evolution of average inbreeding coefficient according to the number of generations considered was also estimated for the current population.

On the basis of the breed origin of each founder (ancestors of the current generation without parents known), contribution of different breeds to each gene pool was computed for the different breeds and groups of breeds, considering either founders or parental origins, that is, origins of parents of individuals of the reference generations. The analyses were performed using the PEDIG software ([http://dga.jouy.inra.fr/sgqa/article.php3?id\\_article=110](http://dga.jouy.inra.fr/sgqa/article.php3?id_article=110), Boichard 2002).

## Results

### Demographic and genealogical parameters

The eight breeds and groups of breeds studied showed a wide range of situations, regarding population size or numbers of breeders (Figure 1, Table 1). Between

2003 and 2010, the number of breeders ranged between 87 (Devon Rex) and 2,428 (PES). Between 2008 and 2010, current generation sizes ranged from 469 (Devon Rex) to 14,921 (PES). On average, sires produced 8.8 kittens, ranging from 5.7 (Devon Rex) to 13.6 (Chartreux), and dams produced 4.7 kittens, ranging from 3.7 (Devon Rex) to 6.2 (Chartreux). We found on average 1 sire for 1.8 dams. All the breeds show good pedigree knowledge ( $EqG = 7.2$  on average), the highest values being found for Birman (8.1) and Chartreux (8.3), while generation intervals ranged from 2.2 (Bengal) to 3.3 years (PES). Between 2003 and 2010, the number of kittens born and used as reproducers followed the same trend as the number of births (Figure S1): on average overall breeds, 17% of kitties (including 5% of male and 12% of female) later became reproducers, the proportion ranging from 11% (Chartreux) to 22% (Bengal).

### Diversity indicators

Table 2 shows the IBD estimators for the eight breeds and groups of breeds/varieties. According to the breed,  $F$  ranged from 2% (Maine Coon) to 4.4% (Chartreux). These inbreeding levels could be explained by pedigree knowledge, population size and also by mating between close relatives (close inbreeding): the proportion of inbred individuals, based on two and three generations, ranged from 2.7 (Maine Coon) to 8.4% (Devon Rex) and from 7.7 (Maine Coon) to 22.5% (Devon Rex), respectively. For each breed considered, there was a large increase in inbreeding coefficients during the first generations (Figure 2). Over the following generations, inbreeding increase was smoother and more regular, indicating no strong bottleneck event.

Average coancestry  $C$  was always lower than inbreeding, which is illustrated by a positive  $F_{IS}$  value for all the breeds, ranging between 0.96% (Maine Coon) and 1.83% (Birman). In BSH and PES groups, average  $\bar{C}$  were lower than 1%, while the maximum value was for the Chartreux breed (approximately 2.8%). Therefore, when using  $C$  instead of  $F$  to compute  $N_e$ , effective population size increased largely, with  $N_{eCi}$  and  $N_{eFi}$  ranging between 127 (Devon Rex) and 1406 (PES) and between 64 (Devon Rex) and 161 (Maine Coon), respectively.

### Gene flow within and between breeds and groups of varieties

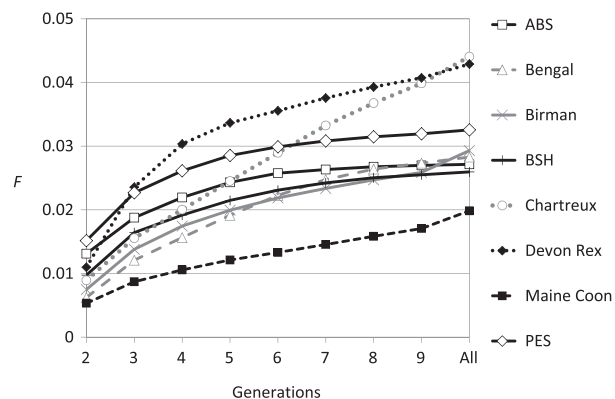
By breed, the proportion of founders originating from outside the breed was variable: based on founder approaches, the contribution of external origins ran-

**Table 2** Genealogical parameters of the breeds considering current generation (2008–2010)

Breed or group of varieties	Nb of individuals	EqG	T	F (%)	$N_{eFi}$	Inbreeding			Coancestry			Main founder origins outside the breed (%)	
						% of individuals inbred after			C (%)	$N_{eCi}$	$F_{IS}$ (%)		Out (%)
						2 generations	3 generations	Overall generations					
Abyssinian/Somali (ABS)	1307	6.31	2.77	2.71	95	6	13.1	67.6	1.14	266	a	0.7	Unknown (0.5)
Bengal	2896	6.68	2.19	2.83	97	3.6	11	95.2	1.78	182	1.07	5.7	American Shorthair (2.2)
Birman	11 109	8.07	3.18	2.93	115	4	13.5	95.1	1.12	365	1.83	5.3	Balinese (2.7)
British Shorthair/ British Longhair/ Highland/ Scottish/ Selkirk (BSH)	6758	6.73	2.69	2.6	105	5.2	13.9	80.7	0.61	553	a	16	Persian (10.5)
Chartreux	6494	8.29	2.9	4.41	78	4.5	13.5	98.5	2.78	146	1.68	11.5	British Shorthair (6.1)
Devon Rex	469	6.47	2.44	4.29	64	5.1	22.5	65.1	2.54	127	1.79	5.9	Burmese (2.6)
Maine Coon	11 642	7.27	2.41	1.98	161	2.7	7.7	91.3	1.03	363	0.96	1.2	Persian (0.9)
Persian/Exotic Shorthair (PES)	14 921	7.39	3.28	3.25	91	8.4	18	88.7	0.26	1406	a	1.7	British Shorthair (1)

EqG, number of equivalent generations; T, generation intervals in years; F, average inbreeding coefficient;  $N_{eFi}$ , inbreeding effective population sizes; C, average coancestry coefficient;  $N_{eCi}$ , coancestry effective population sizes;  $F_{IS}$ , breed fixation index; Out, % of founder origins outside the breed.

aSee Table 3.



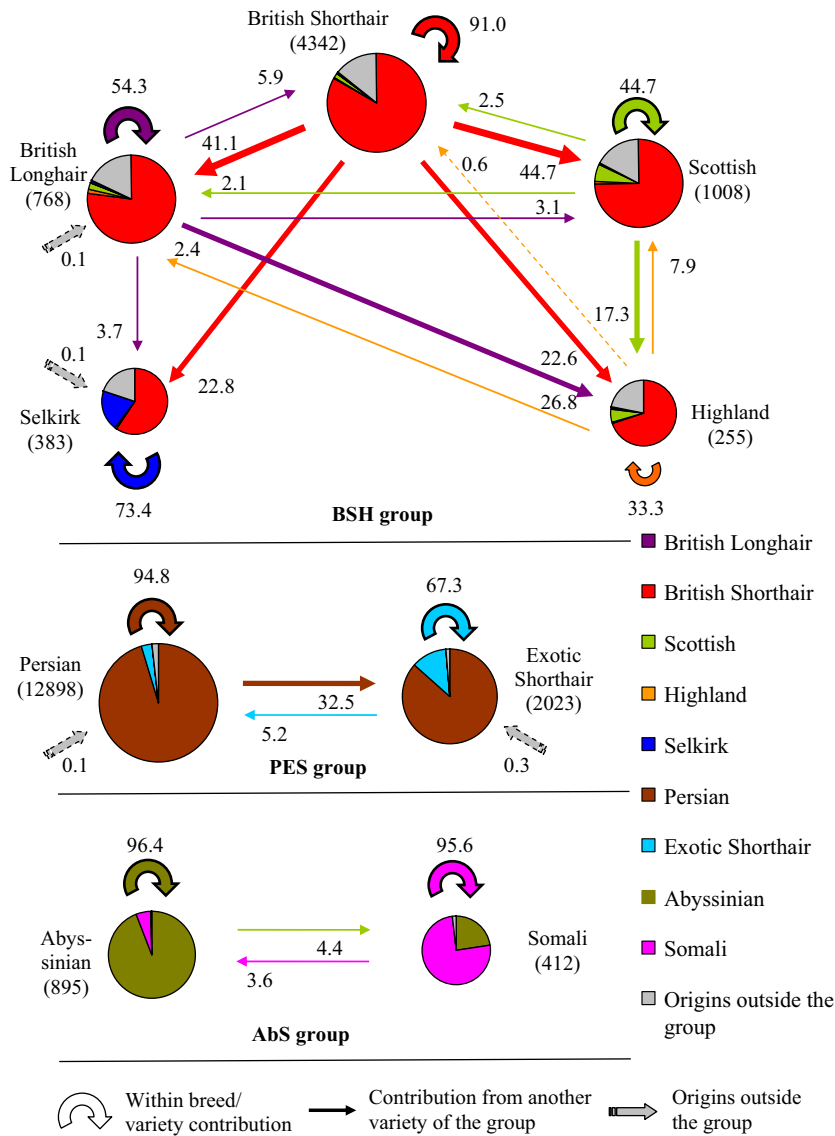
**Figure 2** Evolution of average inbreeding coefficients for the current population according to the number of generations considered. All: all generations considered.

ged from 0.7 (ABS) to 16% (BSH) of the gene pool (Table 2). Most of the time, those external origins were mainly related to one breed: for instance, the British Shorthair contributed up to 50% or more of the external origins for two breeds (namely Chartreux and PES). However, considering the parental origins of the current generation, gene flow was much more limited, and in each population, <1% of those origins belonged to external breeds (Figure 3).

As illustrated by Figure 3, the three groups of varieties show contrasting situations with regard to gene flow among subpopulations. As aforementioned,

in BSH, external origins contributed largely to the gene pool. Within this group, the British Shorthair constituted the largest population (64% of the total population group), and it was also the main origin for the different varieties of the group. Thus, founder origins from the British Shorthair ranged from 59.6% (Selkirk) to 83.1% (British Shorthair) (Table S1). The contribution of the British Shorthair variety remained relatively important even considering its parental origins, with its contribution ranging between 22.6% (Highland) and 91% (British Shorthair) (Figure 3). Within the group, all varieties but one (Selkirk) were involved as contributors of other ones. In the PES group, the Persian constituted by far the main origin, contributing to 86.6% of founder origins of the Exotic Shorthair variety. However, considering the last generation, 67.3% of parental origin in Exotic Shorthair belonged to the Exotic Shorthair. The two varieties of the ABS group constituted more independent subpopulations, with most of the founder and parental contributions in the Abyssinian and the Somali coming from Abyssinians and Somalis, respectively.

According to Table 3, within each of the three groups, the average coancestry was relatively low between each variety, ranging from 0.19 (Abyssinian and Somali) to 0.67% (Scottish and Highland). As expected, the contrast between inbreeding and coancestry was lower when considering each variety



**Figure 3** Founder contributions and parental origins for BSH, PES and ABS groups. Circles indicate repartition of founder contribution according to the probability of gene origins, while arrows represent parental origins (values in%). Sizes of arrows and circles are proportional to contributions and population size (current generation size in parenthesis).

independently than when considering groups of breeds. Indeed  $\overline{F_{IS}}$  values (1.76, 2.96 and 0.69% for BSH, PES, and ABS, respectively, Table S2) were lower than  $F_{IT}$  (2, 3 and 1.59%, respectively),  $\overline{F_{ST}}$  values being contrasted according to groups (0.24, 0.04 and 0.91%, respectively). Yet we noticed that for British Shorthair and Exotic Shorthair varieties,  $F_{IS}$  was slightly higher (2.2 and 3.1%, respectively) than when considering  $F_{IT}$  for BSH and PES groups (2 and 3%, respectively), indicating the existence of a sub-structure remaining among those varieties.

**Discussion**

The aim of this study was to assess genetic diversity and gene flow within and between cat breeds, using, among

others,  $F$ -statistics adapted to pedigree analysis. Cat breeds have rarely been investigated in the past, and the only study based on pedigree analysis (Mucha et al. 2011) showed average inbreeding around 3%, concluding that cat populations are not threatened by negative effects of inbreeding. Considering coancestry as the parameter to minimize for conservational purpose (Baumung & Sölkner 2003), the breeds studied here also show remarkably high levels of diversity, effective population sizes computed based on coancestry ( $N_{eci}$ ) ranging between 127 and 1406. The average coancestry was indeed found to be quite low in comparison with dog breeds. As an illustration, for the eight breeds or groups of varieties, average coancestries ranged between 0.3 and 2.8% (1.4% on average), with current generation sizes ranging from 469 to 14 921 (6949 on



Group of varieties	$F$ (%)	$F_{IS}$ (%)	C (%) within and between varieties				
			British Longhair	British Shorthair	Scottish	Highland	Selkirk
<b>BSH</b>							
British Longhair	2.08	1.24	0.85	0.57	0.5	0.68	0.25
British Shorthair	2.9	2.18		0.74	0.56	0.52	0.28
Scottish	2.12	1.30			0.83	0.67	0.21
Highland	2.18	0.82				1.37	0.22
Selkirk	1.74	-0.20					1.94
<hr/>							
Persian                      Exotic Shorthair							
<b>PES</b>							
Persian		3.23	2.72	0.27		0.21	
Exotic Shorthair		3.4	3.14			0.52	
<hr/>							
Abyssinian                      Somali							
<b>ABS</b>							
Abyssinian		2.44	0.44		1.65		0.19
Somali		3.3	0.02				2.88

$F_{IS}$ , within variety fixation index.

average), with the average  $EqG$  around 7.2. By comparison, in 24 dog breeds with an  $EqG$  larger than 6 (7.1 on average), Leroy *et al.* (2009) found average coancestries to be twice as high (2.8%, ranging between 0.6 and 8.8%), with average current generation sizes approximately 8 times larger (54 645, ranging from 2167 to 156 492). This difference is probably related to the low number of offspring per reproducer in cat breeds. In this study, during a generation interval (around 3 years), sires and dams produced on average 8.8 and 4.7 kittens, respectively. By comparison, in dog breeds (Leroy & Baumung 2011), sires and dams produced 16.4 and 8.3 puppies, respectively, during a generation interval (4 years). The average number of offspring produced per breeder was also on average smaller in cats (12.6 estimated from Table 1) than in dogs (18, see Leroy *et al.* 2009). Therefore, in comparison with dog breeders, a large majority of cat breeders are occasional ones. These breeders used their reproducers with low intensity, the females producing on average one litter during the 2008–2010 period (litter size being found on average around 3.4, data not shown). This has a clear positive impact on genetic diversity, but does not mean that regular bottlenecks do not occur within breeds, which may lead to the dissemination of inherited diseases (Wellmann & Pfeiffer 2009).

In comparison with coancestries (1.4% on average), average inbreeding values were high (3.1% on average), leading to an underestimation of effective population sizes when using inbreeding instead of coancestry (Table 2). These differences, indicating deviations from random-mating conditions and illus-

trated through  $F$ -statistics variations, can be explained by three non-exclusive phenomena: intentional mating between close relatives (close and line breeding), existence of subpopulations (Wahlund effect) and low effective population size.

First, there is a tendency among breeders to plan mating between closely related cats. On average, approximately 5% of kittens were inbred after two generations, meaning their parents were sharing at least one parent. According to an analysis of dog breeds and simulated populations, an increase of approximately 0.7–1% of  $F_{IS}$  could be expected for such a proportion of mating between half- and full-sibs (Leroy & Baumung 2011). This result was in agreement with the large inbreeding increase observed considering the first generations, relative to the following ones (Figure 2).

Secondly, positive  $F_{IT}$  values could also be explained by the existence of more or less differentiated subpopulations within breeds or groups. Two of the three groups of varieties (BSH, PES) show relatively high  $F_{IT}$  values, which could, at first sight, be explained through preferential mating within varieties. As illustrated by Table 3, between-subpopulation coancestry was always lower than within-subpopulation coancestry. However, Figure 3 shows that gene exchanges were relatively frequent among varieties of BSH and PES groups, while in the ABS, only a small proportion of parents originated from the other variety. This was in agreement with the very low  $\overline{F_{ST}}$  values estimated for the BSH and the PES (0.24 and 0.04%) in comparison with the ABS (0.91%) where the level of genetic differentiation between Abyssinians and Somalis was larger.

**Table 3** Average coefficients of inbreeding  $F$  and coancestry  $C$  within and between varieties of BSH, PES and ABS groups

Finally,  $F_{IT}$  and  $F_{IS}$  variations could also be explained by the effective population size of breeds, a limited population size decreasing fixation index and eventually leading to negative values. This phenomenon can be interpreted considering the evolution of IBD estimators. Indeed, in panmixia, inbreeding and coancestry are supposed to differ only by  $\Delta IBD$  (i.e.  $1/(2N_e)$ ), the average coancestry between reproducers corresponding to the average inbreeding of the next generation. This is why, for a given generation and in random-mating conditions at least, we should expect  $C$  to be larger than  $F$ . Therefore,  $F_{IT}$  ( $F_{IS}$  respectively) should tend to decrease in breeds (varieties respectively) with a small effective population size. It may explain the low average  $\overline{F_{IS}}$  (0.69%) in AbS (related to the small population size of Abyssinian and Somali varieties) and therefore the moderate  $F_{IT}$  (1.59%) within the group, despite the large subpopulation differentiation  $\overline{F_{ST}}$  index (0.91%). A small effective population size also explains why the Devon Rex breed, despite the largest proportion of individuals inbred after three generations (22.5%), showed only a moderate  $F_{IS}$  value (1.79%).

In a large group like the PES (considering population size), the high  $F_{IT}$  (3.0%) value estimated was finally less due to the subpopulation differentiation ( $\overline{F_{ST}} = 0.04$ ) than to close inbreeding practices. Indeed, 8.4 and 18% of individuals were found inbred after two and three generations, respectively, explaining the large  $\overline{F_{IS}}$  value (2.96%). By contrast, in the Maine Coon breed, where the smallest proportion of individuals inbred after two and three generations was found (2.7 and 7.7%, respectively), one of the lowest  $F_{IS}$  was also computed (0.96%). These different examples illustrate quite well how the fixation index can be influenced by the breeding practice and the demographic situation of domestic populations.

A comparison between founder and parental origins illustrates the variation in gene flow over time. When considering the parental origins, only a low amount of outcrossing was detected within each breed (implying <1% of parents). Based on these results, we can consider each of the eight populations studied as almost closed, which justifies the grouping choices we made. However, the founder approach results highlight that crossbreeding events have occurred in the past, with more or less important effect on genetic diversity, depending on the breed studied.

The French unified genealogical database was set up in 2000, with founder individuals born during the 1980–2000 period. At this time, each of the breeds and varieties studied were already recognized, which underlines the fact that external contributions are mainly related to recurrent cross-breeding events after

the creation of the breeds. Several explanations can be given for such gene flow. For instance, in the Chartreux breed, the large amount of British Shorthair contribution (6.1%) is probably due to regular registrations of blue British Shorthair individuals within the breed (breeders' personal communication). In the BSH group, breeders in the past have probably used Persian reproducers to improve the quality of their coat, explaining their large contribution (10.5%) as founders. Today, on the basis of the pedigree file, such cross-breeding events rarely occur in France, where they are only exceptionally allowed by LOOF, but may exist in other countries depending on different breeding rules. Development of DNA identification will help to monitor the occurrence of false parentage among cat breeds, as well as the level of introgression of unofficial outcrossings. Studies based on molecular markers may also bring further information on breed relationships. For instance, Lipinski *et al.* (2008) and Kurushima *et al.* (2012) seem to confirm introgression of Persian individuals into British Shorthair populations, as well as British Shorthair individuals into the Chartreux breed. Using molecular markers, Menotti-Raymond *et al.* (2008) were not able to differentiate Exotic/Persian, Abyssinian/Somali and British Shorthair/Scottish varieties. According to the same study, Selkirk was, however, found to be different from British Shorthair and Scottish varieties, in contradiction with our results, given the amount of gene flow observed from British Shorthair to Selkirk varieties. Such discrepancies could eventually be explained by the breeding rules existing in the USA, where only Persian and Exotic Shorthairs are permitted for cross-breeding with Selkirk individuals.

From a practical point of view, the  $N_{eCi}$  values, found larger than 100 for each of the breeds studied, indicate that those populations are probably submitted to a limited genetic drift. By contrast, the large inbreeding values, connected to lower  $N_{eFi}$ , may increase the proportion of individuals affected by monogenic recessive genetic disorders, in relation to their allele frequency (Leroy & Baumung 2011). Some measures should therefore be recommended to limit close inbreeding practices, at least for breeds with  $N_{eFi}$  lower than 100, and particularly for Devon Rex, where 22.5% of individuals were inbred after three generations.

## Conclusions

To conclude, we can state that cat breeds constitute populations submitted to relatively low selection intensity, with various levels of genetic structure, according to breeding practices and/or the existence

of varieties, involving more or less important gene flow within a given population. If at the population level, genetic drift is expected to be limited, high individual inbreeding level found by contrast led us to recommend that particular attention should be paid to population structure and inbreeding practices.

Each of the breeds studied has been submitted to cross-breeding events in the last 30 years, with different impacts on breed genetic diversity. Yet, the eight populations studied are currently almost closed to foreign influence, with, however, regular gene flow remaining among varieties. Studies like this one may provide useful information to define current population subdivisions more clearly. They also give insight into former gene flow, which could be useful for gene association studies (Quignon *et al.* 2007) or when considering authorization of new cross breed events. Cross-breeding may constitute an interesting option for introducing genetic diversity within a given breed and/or improving it, especially in relation to its health status. Further studies could consider more widely the potential impacts of those breeding practices (close breeding, line breeding and outcrossing) on animal welfare and health.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Evolution of number of reproducers born and used according to breeds over the 2003–2008 period.

**Table S1** Origins of founders among varieties of BSH, PES and ABS groups.

**Table S2** Fixation index for BSH, PES and ABS groups.