

Dispersal pattern of domestic cats (*Felis catus*) in a promiscuous urban population: do females disperse or die?

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Summary

1. The domestic feral cat (*Felis catus* L.) is a good model for studying intraspecific variability of dispersal patterns in mammals because cats live under a large diversity of socio-ecological conditions. We analysed both the natal and breeding dispersal patterns of domestic cats in a promiscuous urban population and tested whether or not it differed from the male-biased natal dispersal pattern observed for polygynous rural populations.
2. During an 8-year study we recorded the exact date of *in situ* death for 148 marked cats and the exact date of disappearance from the population for 99 other cats. Because undiscovered deaths might over-estimate dispersal probabilities when considering only disappearance probabilities, we made an novel application of multistrata capture–recapture methods in order to disentangle dispersal from true mortality.
3. We showed that mature females dispersed, both before and after their first reproduction, at 1 and 2 years old. Contrary to females, no dispersal seemed to occur in males. Before sexual maturity, females that disappeared at 1 and 2 years old were in worse body condition than females that stayed in the population area after 2 years old. However, they did not reproduce less successfully before their disappearance than females that died later in the population area.
4. The female-biased and low natal dispersal pattern in this population was atypical compared to other promiscuous/polygynous mammals and differed from that observed in rural polygynous populations of domestic cat. Neither local mate competition nor inbreeding avoidance appeared to be sufficient pressures to counterbalance ecological constraints on dispersal in an urban environment. However, local resource competition for den sites between potential matriarchies could lead to the breeding dispersal of less competitive females.

Key-words: breeding and natal dispersal, capture–recapture, *Felis catus*, inbreeding avoidance, local competition.

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Introduction

Why animals move before their first reproduction or between two successive breeding stages (Howard 1960; Greenwood 1980) has been the subject of intensive debates during the last two decades (Dobson 1982; Johnson & Gaines 1990; Wolf 1993; Clobert *et al.* 2001). In mammals, a large variability of non-exclusive proximal and ultimate causes of dispersal [e.g. local

resource and mate competition (Dobson 1982; Favre *et al.* 1997; Berteaux & Boutin 2000), close inbreeding (Greenwood 1980; Wolff 1993) or territory bequeathal to the offspring (Berteaux & Boutin 2000)] occurs both between and within species (Pusey & Packer 1987a,b), and also between sexes within a species (Holekamp 1984). As a consequence, dispersal patterns in mammals vary considerably in terms of amount (Waser 1996), timing and age of emigration (Arnold 1990) in dispersal distances (Van Vuren 1998), as well as in direction and amplitude of the sex-bias (Dobson 1982). It is well known that the mating system is linked strongly to the sex-biased natal dispersal pattern in mammals at the interspecific level (Greenwood 1980; Dobson 1982; Perrin & Goudet 2001): polygynous/promiscuous mating systems with female-defence by

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males are associated with male-biased dispersal, whereas monogamous mating systems are related to similar dispersal probabilities in both sexes (Greenwood 1980; Dobson 1982). Nevertheless, beyond this general pattern, intraspecific variability of dispersal patterns, and in particular of natal dispersal pattern, occurs regularly both over time in one population and from one population to the other for a given species (Waser 1996). Identifying the main biodemographic factors that structure this intraspecific variability of dispersal patterns appears necessary to gain a better understanding of evolution of dispersal behaviour within and across taxa.

In this paper, we studied the dispersal pattern of a high-density population of feral cats (*Felis catus* L.) and compared our results with the dispersal pattern reported in lower-density cat populations (Liberg 1980; Liberg *et al.* 2000). Cats live over a wide range of contrasting ecological conditions. Depending on the resource distribution, they form larger or smaller groups characterized by different social and spatial structures, but also by different mating systems (see Liberg *et al.* 2000 for a review). In rural environments, cats live at lower densities than 2.5 cats ha⁻¹ (Liberg *et al.* 2000). They are generally solitary, but females can sometimes live in small groups of close-related individuals. A few territorial males defend access to females living on their large non-overlapping home ranges, leading to a strong polygynous mating system (Liberg 1980; Pontier & Natoli 1996; Say, Pontier & Natoli 1999). In agreement with theoretical predictions (Dobson 1982; Perrin & Goudet 2001) the natal dispersal pattern is strongly male-biased (Liberg 1980), whereas no breeding dispersal events have been recorded. Density is much higher in urban populations than in rural ones and can reach more than 10 cats ha⁻¹ (Liberg *et al.* 2000). Cats form large multimale-multifemale social groups known as colonies (Liberg *et al.* 2000). They live on small overlapping home ranges and share the resources available (in particular food and shelter). The mating system is promiscuous (Natoli & De Vito 1991; Say *et al.* 1999). Although a male-biased dispersal pattern is expected in populations characterized by such a promiscuous mating system (Greenwood 1980; Dobson 1982), no evidence was reported for male-biased natal dispersal or for breeding dispersal in large urban populations of domestic cats.

Here, we gathered information during an 8-year study of marked animals living in a high-density population in the city of Lyon (France) to test whether urban cats show a male-biased natal dispersal pattern, as expected by theoretical models, as well as occurrence of breeding dispersal events. We used an indirect approach based on multistrata capture-recapture data analysis applied to disappeared and dead individuals in order to disentangle dispersal from true mortality. We tested for age and sex effects on dispersal probabilities. We also characterized dispersers with respect to body condition and reproductive status in order to

infer the ultimate causes of dispersal from proximal factors. Indeed, these two characteristics are assumed to be important proximal factors able to provoke emigration: body condition is a major component in the ability to compete for resources and sexual partners (Clutton-Brock 1988) and unsuccessful reproduction is a cue for future reproductive success (e.g. in birds: Switzer 1997; Haas 1998).

Materials and methods

MONITORED POPULATION

The studied population of 70 feral cats resides in a hospital park in the centre of Lyon (France). The hospital area is 7.2 ha and is bounded by walls, buildings and busy traffic roads. Cats were fed mainly with canteen waste by hospital staff, but they could hunt birds and small rodents anywhere. Groves and cellars of the hospital are used as shelters by the cats. From 1992 cats were monitored for demography, epidemiology, spacing pattern and behaviour. Parentage genetic analysis was also studied between 1995 and 1998 using microsatellite markers (Say *et al.* 1999; Say, Pontier & Natoli 2001). All cats were recognizable individually by sight from their coat colour, pattern and hair length, or a coloured collar. Density of cats was 9.7 ± 0.5 cats ha⁻¹ depending on the year. Adult sex ratio was balanced during the study with, on average, $48 \pm 2\%$ of adult males (Say 2000). Cats formed a large stable social group characterized by a dominance hierarchy both for females and males (Say *et al.* 2001), as has been described in other such high-density populations (Natoli & De Vito 1991). Relationships between members of the colony were generally amicable and open aggression was very rare (Natoli & De Vito 1991; Say *et al.* 2001). Female oestrous is generally synchronized (Say *et al.* 2001; see also Liberg *et al.* 2000). Reproductive females produced one or two litters each year of, on average, three to four kittens (Say 2000). During the reproductive period, several males court a receptive female simultaneously. They do not interact aggressively and copulate with the receptive females one after the other (Natoli & De Vito 1991; Say 2000). As a result, a promiscuous mating system characterized by a very high rate of multiple paternity occurs (in 80% of litters kittens were sired by at least two different fathers; Say *et al.* 1999). In contrast to rural populations, where age at first reproduction for males is delayed well after physiological maturity (Liberg 1980; Say *et al.* 1999), age at first reproduction corresponds to age at physiological sexual maturity for both sexes in this colony (between 6 and 9 months for females and 9–12 months for males; Say *et al.* 1999).

RECORDED DATA

Cats were trapped using double-door metal traps three times in 1993, once in 1994, and from 1995 trapping

sessions were standardized to twice a year. Ninety per cent of the approximately 500 trapped cats during this period were captured first in their first year, most of them when they were less than 6 months old. During each trapping session cats were handled, then anaesthetized with an intramuscular injection of Ketamin Chlorhydrat (Imalgène 1000 15 mg/kg, Rhône Merieux, Lyon, France) and Acepromazin (Vétranquil 5.5% 0.5 mg/kg, Sanofi, Paris, France). Age was estimated from dentition (Pascal & Castanet 1978) for individuals trapped first at more than 1 year. It was known precisely for the cats first trapped as juveniles. A permanent subcutaneous electronic device (transponder Trovan, AEG & Telefunken Electronic, UK) and a coloured collar was fitted to aid subsequent identification of each individual. During each trapping session, all cats that were untrapped but seen on the site were recorded as trapped. From the second half of 1996 monitoring pressure increased, and we were present at the study area at least 1 day per week. This allowed us to determine precisely the time of disappearance (real dispersal and unrecovered death) and *in situ* known death (recovered death) of individuals. No information about death outside the population area was available.

DATA ANALYSIS

Dead or disappeared: multistrata design

CMR methods are now well established (see Lebreton *et al.* 1992 for a review), so they will not be described in detail. However, we emphasize a specific point of our approach. When applied to a single study site, capture–recapture models provide estimates of apparent survival probability, because animals which were never recaptured in the study area could have died or dispersed (Lebreton, Pradel & Clobert 1993). In order to disentangle dispersal from mortality, we used multistrata capture–recapture models (Arnason 1973; Hestbeck, Nichols & Malecki 1991; Brownie *et al.* 1993) and defined two theoretical strata in our analysis. The first was called the ‘disappeared stratum’ and was built from disappeared individuals from the hospital park. Because the recapture probability was very close to 1, we defined an individual as disappeared if it was not seen or recaptured in the 6 months following its estimated disappearance date, corresponding to one time interval between two trapping sessions. The disappeared stratum allowed us to estimate the apparent survival probability, which is an under-estimate of the true survival probability because disappeared individuals could have either died and not yet have been recovered or dispersed outside the study area (Lebreton *et al.* 1993). The second stratum was built from discovered dead individuals and was called the ‘dead stratum’. The dead stratum allowed us to estimate the true survival probability because dead individuals recovered in the population area clearly did not emigrate. Therefore, if no significant emigration

occurred in a given sex- and age-class, estimation of the survival probability for this sex- and age-class should not differ between the two strata. In contrast, if dispersal occurred for a given age- and/or sex-class, we expected the estimated survival probability to be significantly lower for the disappeared stratum than for the dead stratum. We made two implicit assumptions when comparing the disappeared stratum and the dead stratum to assess the predominant age- and sex-classes which emigrate: first, that dead cats would not have disappeared if they had survived and secondly, that cats which disappeared had the same survival probability as dead cats before they die. These two assumptions are common when studying dispersal because we never know what dispersed or disappeared individuals would have done if they had stayed.

Because disappeared animals could be dead, we had to take into account the recovery probability of dead individuals when adjusting survival probability in the disappeared stratum. To do that, we used multistrata models with live and dead encounters, $S(\cdot)P(\cdot)\psi_{AB}(\cdot)r(\cdot)$, where S is the survival probability, P is the capture probability, ψ_{AB} is the probability of transition between two strata A and B, and r is the recovery probability (Hestbeck *et al.* 1991; Brownie *et al.* 1993; Burnham 1993). We assumed that the two strata corresponded to two different and theoretical birth states: the first could be interpreted as a state of a ‘future disappeared’ animal and the second as a state of a ‘future philopatric’ animal. Because these two states were exclusive, we set to zero all transition probabilities of the multistrata models. We then tested for a stratum-effect on survival probabilities to detect predominant sex- and/or age-disperser classes.

SELECTED INDIVIDUALS

Data presented here were recorded from January 1993 to April 2001, representing 17 trapping sessions. We excluded all animals that were either not captured first in their first year of life, or that were not born in the population. A total of 99 animals (57 males, 42 females) composed the disappeared stratum and 148 animals (78 males, 70 females) composed the dead stratum. Capture and survival probabilities were constrained to equal zero, respectively, for the final and the penultimate trapping sessions when time and stratum effect were adjusted on the data set for dead stratum (i.e. cats that died between the last two trapping sessions could not be recaptured alive at the last trapping session). In the same way, capture probability for the disappeared stratum was also set to zero for the last trapping session.

GOODNESS-OF-FIT

We used the Cormack–Jolly–Seber model (CJS; $S(t).P(t)$) as a general model to start from using new implementations of goodness-of-fit tests proposed by

Table 1. Subscripts and biological significance of models used for modelling survival, capture, transition and recovery probabilities in the Croix-Rousse population of domestic cats

Notation	Biological significance
(.)	Constancy over time and with age and/or sex
(0)	Fixed parameter to a given value
(t)	Time-dependence
(sex) or (stratum)	Single effect of sex or stratum
(a)	Age-dependence in years
(2ac)	Two age-classes (juveniles and adults)
(3ac)	Three age-classes (juveniles, young adults of 1 and 2 years, old adults of at least 3 years)
(a + t)	For example, additive effect of age and between-years variations Such effect is valuable for any combination of factors (age, sex, time and stratum)
(sex*stratum)	Double interaction between sex and stratum for example Such effect is valuable for any combination of factors (age, sex, time and stratum)
(a*sex*stratum)	Triple interaction between any age class, sex and stratum.

U-CARE software (Choquet *et al.* 2001). Because to our knowledge no single test exists for multistrata designs, we tested the CJS model in each of the four stratum–sex associations. We assumed that if the CJS model fit all four of the data sets, then the overall data set should be fitted well by the CJS model.

SURVIVAL ANALYSIS

We used a three-step approach to analyse the survival pattern of the population. We tested first for age, sex and time effects on recovery probabilities using the whole data set (disappeared and dead individuals) and considering time-dependence on survival probability and a constant capture probability, whereas transition probabilities were set to zero, as mentioned above. Indeed, because the first stratum is composed only of disappeared individuals and the second is composed only of dead and recovered individuals, recovery probabilities were by construction 0 for the disappeared stratum and 1 for the dead stratum, when considered independently. In the second step, we tested for age, sex, stratum and time effects on capture probability using the previous best selected model for recovery probability, time-dependence on survival probability and fixed the transition probability to 0. In the third step, survival probabilities were fitted using previous adjusted capture and recovery probabilities. Because our aim was to detect sex, age and stratum effect on survival probabilities, we did not test for the combination between time and other effects (sex, age, stratum) on survival probabilities.

Thereafter, we looked for the best age- and sex-dependence model using different hypotheses about age structure (Table 1): (1) a model with two age-classes, to test whether or not juvenile survival (< 1 year old) was equal to adult survival; (2) a model with three age-classes corresponding to juveniles, young adults (1 and 2 years old) and old adults (more than 3 years old); and (3) a model with continuous age in years (less than 1 year old, 2 years old, 3 years old and more than 4 years old). The same age structures were

used for fitting the recovery and capture probabilities. We tested finally for the interaction between stratum and the best previous adjusted sex and age effects on survival probabilities. Where this last interaction was significant, we looked for the age- and/or sex-classes for which survival probabilities were different regarding the stratum: we then considered these age- and/or sex-classes as the predominant dispersers ones if survival probability was significantly lower in the disappeared stratum than in the dead stratum.

For each of the three steps of the analysis, we followed Lebreton *et al.* (1992) for selecting the most parsimonious model using the Akaike information criterion (AIC, Burnham & Anderson 1992). We used the AICc (sample-size-adjusted AIC, Anderson, Burnham & White 1994) to take into account low effective sample size. The best approximating model has the lowest AICc. We also used LRT to test for specific biological effects in nested models. All survival probabilities were standardized to annual survival to take into account differences in interval length between two trapping sessions over time. We used MARK 2.1 software (White & Burnham 1999) for all analyses.

DISPERSERS' CHARACTERISTICS

When sex- and/or age-classes were identified as predominant dispersers, we tested whether these individuals differed with respect to body condition and reproductive status. We compared all individuals belonging to the sex- and/or age-class which was assumed to have dispersed with the same class of individuals which stayed and died later in the population area.

Body condition was assessed before sexual physiological maturity to test for the influence of early body condition on dispersal. Because animals were not all captured at the same age, we derived a body condition index from the regression of the logarithm of body mass against the logarithm of age in months for individuals between 1 month and 6 months only, i.e. during the linear phase of the growth curve (Deag, Manning

& Lawrence 2000). Individuals with positive residuals were assumed to be in good condition, whereas individuals having negative residuals were assumed to be in poor condition. We tested both for the relation between age and body mass in logarithm and for the stratum effect on juvenile body condition index with an ANCOVA (SPLUS software, Venables & Ripley 1999) Reproductive output of females was determined using both behavioural and genetic data (see Say 2000; Say *et al.* 2001). A female was defined as having reproduced successfully when at least one of its kittens reached the age of 2 months (corresponding to successful weaning; Deag *et al.* 2000). We tested whether unsuccessful reproduction could be a proximal factor of female disappearance by comparing: (1) the reproductive output of the females disappeared during their third year of life; and (2) the reproductive output, measured at the end of the third year of life, of the philopatric females remaining in the population after 3 years. As the philopatric females benefited from 2 years of reproductive activity, in the disappeared stratum we selected only those females which disappeared in their third year of life in order not to under-estimate the reproductive output of the disappeared females, due to the lowest period of reproductive activity in the population. We compared the two groups with Fisher's exact test. As males have no information on their reproductive success, the same analysis was not possible for males.

Results

GOODNESS-OF-FIT TESTS

The overall goodness-of-fit test led us to accept the CJS model for the disappeared females group ($\chi^2 = 2.18$, $P = 0.99$, d.f. = 10), and both for the dead males and disappeared males groups (respectively, $\chi^2 = 4.83$, $P = 0.96$, d.f. = 12 and $\chi^2 = 6.31$, $P = 0.71$, d.f. = 9). However, the overall goodness-of-fit test led us to reject the CJS model for the dead females group ($\chi^2 = 30.18$, $P = 0.005$, d.f. = 13). The test components of the overall test showed that the main part of the χ^2 value came from only two single components (test 3SR at the seventh and eighth trapping sessions with, respectively, 15.37 and 7.14 χ^2 statistic values with 1 d.f. each). This result implies that females captured at these trapping sessions had a lower probability of being recaptured later compared to females that had been captured during the previous trapping sessions. Following the procedure of Choquet *et al.* (2001), removing these two components led to an overall goodness-of-fit χ^2 test equal to 7.77 with d.f. = 11 ($P = 0.73$). We thus accepted the CJS model as the general model from which to start the survival analysis.

MODEL SELECTION

The model with three age-classes and the model with an interaction between three age-classes and sex on

Table 2. First step: model selection for the recovery probability r with $S(t)$, $P(\cdot)$ and all transition probabilities $\psi(0)$ set to zero (see Methods). Second step: model selection for the capture probability P with $S(t)$, $r(3ac*sex)$ (see first step of the table) and all transition probabilities $\psi(0)$. Only the six best models are shown in the table. The model in bold is the selected model for the following steps of analyses. Model deviances were calculated as $-2\log(\text{Likelihood})$ of the models considered. AICc values were calculated using the number of separately identifiable parameters. We report ΔAICc , the difference between AICc for each model and that for the model with the smallest AICc in the set of models considered: best models have also the lowest ΔAICc

Models	No. identifiable	Model deviance	ΔAICc parameters
First step: recovery probability			
$r(3ac)$	20	1008.84	0
$r(3ac*sex)$	23	1003.36	1.03
$r(3ac + sex)$	20	1012.21	3.37
$r(2ac)$	19	1016.07	5.07
$r(2ac*sex)$	21	1014.61	7.93
$r(t)$	32	990.70	8.35
Second step: capture probability			
$P(\cdot)$	23	1003.36	0
$p(sex)$	24	1001.35	0.17
$P(2ac)$	24	1002.20	1.03
$p(stratum)$	24	1002.26	1.08
$P(3ac)$	25	1001.73	2.74
$P(sex*stratum)$	26	999.95	3.17

recovery probabilities fit the data equally well (difference of AICc values lower than two points, Burnham & Anderson 1998; Table 2), and thus no significant sex effect was detected on recovery probability (LRT, $\chi^2 = 5.478$, $P = 0.14$, d.f. = 3). As we wanted to test for specific hypotheses about sex and age effects on survival probabilities, we none the less used the model with $r(3ac*sex)$ for further analysis in order to increase the accuracy of the estimations.

In the second step of the analysis we selected the model with constant capture probability, even though the three models with sex effect, with two age-class effects and with stratum effect had similar values of AICc (Table 2). This choice was made because sex, age and stratum effects were due to the same two disappeared male individuals which were not recaptured at one trapping session but were recaptured at subsequent ones. Estimation of capture probability was 0.995 ± 0.004 (SE). This value indicated that emigration, if it occurs, is permanent.

We then fitted the survival probabilities in the third step of the analysis. We tested for the best triple interaction between age, sex and stratum using the three age-structures defined above (continuous age, two and three age-classes, Table 3). The best model was the one with three age-classes, $S(3ac*sex*stratum)$, even though the model with only two age classes fitted the data as well ($\Delta\text{AICc} = 1.76$). We then tested for stratum, age and sex effects (Table 3). Effect of age and sex were

Table 3. Model selection for the survival probabilities with $r(3ac*sex)$ and $P(.)$ (see Table 2) and all transition probabilities $\psi(0)$

Models	No. identifiable parameters	Model deviance	$\Delta AICc$
S(3ac*sex*stratum)	19	968.06	0
S(2ac*sex*stratum)	15	978.36	1.76
S(3ac*stratum)	13	985.06	4.24
S(a*sex*stratum)	23	964.38	4.98
S(2ac*sex)	11	1009.12	24.12
S(a + sex)	12	1007.32	24.41
S(3ac + sex)	11	1010.61	25.61
S(t*sex)	36	957.67	27.36
S(2ac)	9	1017.33	28.17
S(3ac*sex)	13	1009.19	28.38
S(a*sex)	15	1005.58	28.98
S(a)	11	1015.12	30.12
S(3ac)	10	1018.09	31.01
S(stratum*sex)	11	1018.63	33.63
S(2ac + sex)	10	1021.10	34.02
S(3ac + stratum)	11	1019.08	34.08
S(stratum + sex)	10	1025.06	37.98
S(t)	23	1003.36	43.97
S(.)	8	1049.08	57.85

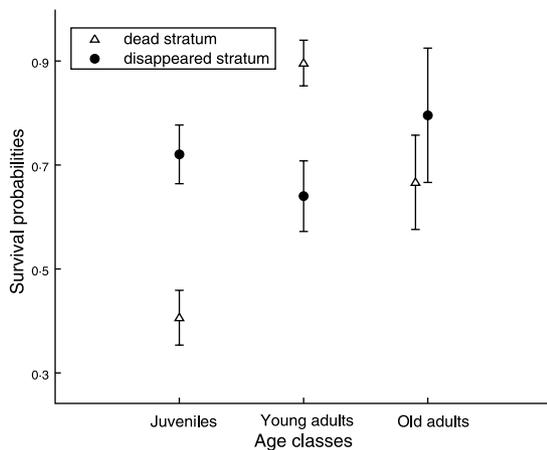


Fig. 1. Age effect on survival probabilities of females (\pm SE) in disappeared stratum ($n = 42$) and dead stratum ($n = 70$) in the urban population of Croix-rousse Hospital [model $S(3ac*sex*stratum)p(.)\psi(0)r(3ac*sex)$].

significant ($\Delta AICc = 33.63$, $\chi^2 = 50.57$, $P < 0.0001$, d.f. = 7, $\Delta AICc = 4.24$, $\chi^2 = 16.99$, $P = 0.005$, d.f. = 5, respectively, Table 3). We finally tested for the stratum effect to assess the occurrence of dispersal comparing models, $S(3ac*sex*stratum)$ and $S(3ac*sex)$: stratum had a strong effect on survival probabilities ($\Delta AICc = 28.38$, $\chi^2 = 41.14$, $P < 0.0001$, d.f. = 5; Table 3, Figs 1 and 2). Model $S(3ac*sex*stratum)$ was thus selected for assessing sex and age effect on dispersal probability. Given both the values of the estimation of survival probabilities (Figs 1 and 2) and our theoretical expectations, only females belonging to the second age-class (1- and 2-year-old females) could be presumed to be predominant dispersers in our population.

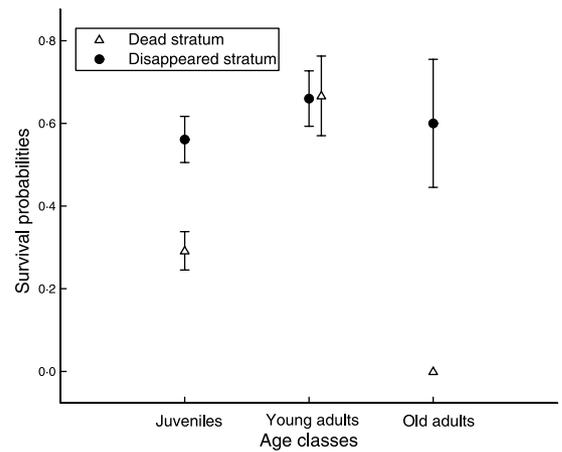


Fig. 2. Age effects on estimated survival probabilities of males (\pm SE) in disappeared stratum ($n = 57$) and dead stratum ($n = 78$) in the urban population of Croix-rousse Hospital [model $S(3ac*sex*stratum)p(.)\psi(0)r(3ac*sex)$]. Estimation of the survival probability to zero of the old adults age class in the dead stratum was due to the fact that only two males in this stratum survived to 3 years old and then died before they were 4.

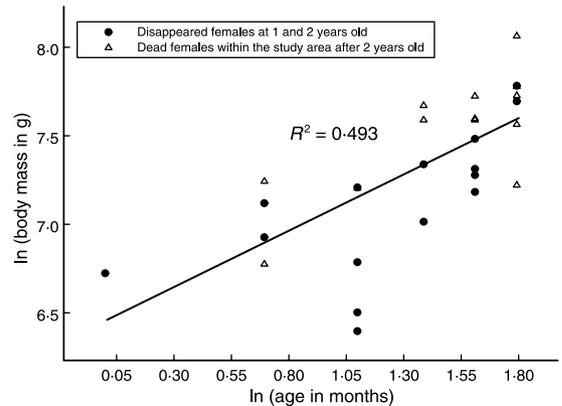


Fig. 3. Age-independent body condition index.

BODY CONDITION AND REPRODUCTIVE OUTPUT OF THE DISAPPEARED FEMALES

We then tested whether 1–2-year-old females that disappeared from the colony differed with respect to juvenile body condition and reproductive status before age 2 from 1–2-year-old females that stayed within the colony after 2 years.

The relationship between body weight and age was the same for females belonging to the two groups of females (ANCOVA: $F = 0.11$, d.f. = 1, $P = 0.74$). Body mass was correlated positively with age in females before sexual physiological maturity (ANCOVA: $F = 25.4$, d.f. = 26, $P < 0.0001$, Fig. 3). The 1–2-year-old females that disappeared had a significantly lower mean juvenile body condition than females that lived and died within the hospital park after 2 years (ANCOVA: $F = 6.38$, d.f. = 26, $P = 0.018$).

The probability of having had at least one successful reproduction at the end of the third year of life did not differ between females that disappeared during their

third year of life and philopatric females belonging to the dead stratum (Fisher's exact test, $P = 0.38$, $n = 15$; reproductive status was recorded at 36 months for the philopatric females).

Discussion

When studies concern only one focal population, biologists are faced with the impossibility of disentangling permanent emigration from the population area and unrecovered *in situ* mortality (Lebreton *et al.* 1993). We made a novel use of multistrata capture–recapture methods to resolve these problems. In our approach, we assumed that survival probabilities estimated from the dead stratum should always be at least as high as survival probabilities estimated from the disappeared stratum. Nevertheless, we found that the survival of juveniles was lower in the dead stratum than in the disappeared stratum for both sexes (Figs 1 and 2). This unexpected result was due to the fact that the < 2-month-old cats that disappeared (i.e. before weaning) were classified systematically as belonging to the dead stratum. We would then have over-estimated survival probabilities of juveniles in the disappeared stratum, as mortality occurs principally before weaning in young mammals (Caughley 1966). Consequently, natal dispersal before physiological sexual maturity could not be studied correctly and precisely. Concerning adult males, no evidence of dispersal occurred at any age of cats. In contrast, mature females seem to disperse at 1 and 2 years old: the survival probability in the disappeared stratum was lower than that reported in the dead stratum. Female dispersal occurs both before and after known successful reproduction, suggesting breeding dispersal rather than natal dispersal. Nevertheless, dispersal rates as well as immigration rates seemed to be low; less than 12% of the overall population disappeared each year and only five immigrants were recorded during the study period.

Even if natal dispersal before 1 year old could not be assessed precisely, such a dispersal pattern (weak and female-biased dispersal) differs strongly from well-known interspecific model expectations (Dobson 1982; Perrin & Goudet 2001) but also from the dispersal pattern observed in rural polygynous populations of domestic cats (Liberg 1980; Liberg *et al.* 2000), and the pattern reported commonly in polygynous/promiscuous Felids or other mammals (Pusey & Packer 1987a; Smith 1993; Waser 1996). Domestic cats thus show intra-specific variability of dispersal patterns related to change in environment, density, mating system and social organization (Say *et al.* 1999; Liberg *et al.* 2000).

In a Swedish rural low-density population (three cats km⁻²), Liberg (1980) reported that 87% of young males left their mother's home-range after physiological maturity at between 1 and 3 years in response to high level of aggression received from dominant territorial males. In contrast, 74% of the females were philopatric (Liberg 1980). Liberg then assumed that local mate

competition, associated with between-sex difference in parental investment, led to between-sex differences in dispersal costs and benefits of philopatry (Greenwood 1980; Dobson 1982) and suggested that this is the primary factor which drives male dispersal in rural populations. In contrast to rural populations, among males aggression and variance of male reproductive success are low in high-density urban populations: high-ranking males do not defend access to females and young males can reproduce successfully as soon as they reach physiological sexual maturity (Say *et al.* 1999, 2001; Natoli & de Vito 1991; Yamane 1998). Local mate competition between males is much lower than in rural populations and is unlikely to be strong enough to lead to emigration of males. Disentangling the mating system from the type of resources then defended appear crucial in order to predict dispersal patterns (Greenwood 1980; Perrin & Goudet 2001).

Inbreeding avoidance is assumed, equally, to be a main ultimate cause of dispersal in social mammals (Greenwood 1980; Wolff 1993; Perrin & Goudet 2001), but is probably not responsible for the dispersal pattern reported in this urban cat population. Indeed, most males and females stay on their birth site and because of overlapping generations, they could potentially mate with close relatives. Genetic determination of paternity showed that highly inbred mating occurred in our population (mother–son, father–daughter and brother–sister; Say, Devillard & Pontier, unpublished results; see also Macdonald *et al.* 1987 and Ishida *et al.* 2001 for similar observations) without any decrease of litter size, survival probabilities or body weight of the offspring (Say & Pontier, unpublished). These results suggest that there are low costs of inbreeding in domestic cats and that inbreeding is probably insufficient to drive dispersal in both sexes.

Local resource competition is the third ultimate cause usually cited to explain dispersal pattern (Favre *et al.* 1997). Because food is given in profusion by the staff of the hospital and non-empty bowls are often observed the following day after they were filled, we think that competition for food is weak in our population. Our hypothesis is supported by the good body condition of cats in this population. However, the number of parturition sites could be limited. As kittens are born blind with low mobility and thermoregulation capacities, their survival depends on maternal care and on the capacity of the female to find a nest which will protect young successfully from predators, conspecifics and climatic conditions. Female reproductive success suffers dramatically from poor access to the best nest sites (Macdonald *et al.* 1987) and local resource competition for good sites can be very strong (Macdonald *et al.* 1987; Liberg *et al.* 2000); all the more so as each female is not a sole competitor in the social group but represents a potential matriarchy if she gives birth. Dominant or older females are able to influence which females are allowed to stay in the central zone (nearest the resource centre, Macdonald *et al.* 1987; Liberg *et al.*

2000), even if subordinate females are younger sisters (Liberg *et al.* 2000). Thus, females that are excluded from the central zone have to endure worse den sites, less communal rearing and perhaps more aggression towards them, leading to dispersal to find a better reproductive environment. This idea of forced dispersal of females is not consistent with the hypothesis that dispersal is driven by local resource competition and seems voluntary and opportunistic in this sex (Liberg *et al.* 2000).

The females that disappeared from our colony had a significantly lower juvenile body condition than females that lived and died within the hospital park. They did not suffer from lesser access to food and were not more infected by the feline leukaemia virus (FeLV) (Fisher's exact test, $P = 0.358$, $n = 35$), which is one of the main mortality causes, with poisoning and road accidents, in urban populations (Romatowski 1995) before their disappearance. Disappeared females could thus be considered as dispersers rather than unrecovered dead individuals. As body mass and body condition strongly influence competitive abilities and successful reproduction in mammals (Clutton-Brock 1988; Gaillard *et al.* 2000), it is reasonable to think that lighter females could be poorer competitors for den sites and could then disperse to find a better reproductive environment. Such a trend has been observed, for example, in birds whose body condition during the first month of life is correlated positively with the quality of the future breeding habitat (Verhulst, Perrin & Riddington 1997). Nevertheless, if female cats in high-density populations disperse mainly to find a better reproductive environment, it is surprising to find that the reproductive success of disappeared females before their disappearance was the same as philopatric females at the same age. However, our measure of reproductive success is approximate and told us nothing about reproductive costs. Indeed, the reproductive costs for disappeared females could nevertheless be higher, due to their potential lower body condition at first reproduction.

In conclusion, our results showed an atypical pattern for a promiscuous mammal (Greenwood 1980; Dobson 1982). In this cat population, both sexes seemed highly philopatric and the main dispersing sex was the females. It appeared that any ultimate costs of philopatry seemed to be sufficient to exceed probable high costs of dispersal due to strong ecological constraints (highly used roads and high patchy resource distribution; Pontier 1993), leading to an uncommonly reported dispersal pattern in a polygynous/promiscuous mammals. However, breeding dispersal of females could be explained by local resource competition for den sites, stimulating females to find better reproductive conditions. Large social multimale-multifemale populations are very recent in cats (about 50 years), and the ancestral model is obviously the rural polygynous cat (Liberg *et al.* 2000). The time separating rural polygynous to urban promiscuous cat populations is perhaps too short to

allow evolutionary pressures to act. It is possible, then, that the urban cat corresponds to a 'transition' stage in this species. If this is the case, domestic cats would be an example of phenotypical plasticity in dispersal behaviour because such a behaviour does not occur when environmental conditions change (Murren *et al.* 2001).

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