

On the use of pharmacological sterilisation to control feral pigeon populations

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Abstract. The use of chemosterilisation for controlling feral pigeon populations was investigated by: (1) quantifying the reproductive activity of pigeons in two Italian cities; (2) testing the efficacy of nicarbazin, an anticoccidial drug with rapid and reversible effects on the reproduction of laying hens, on groups of paired pigeons maintained in open aviaries; and (3) simulating the effects of the use of nicarbazin on a hypothetical population, allowing for the reproductive productivity recorded in (1) and the efficacy of this drug as obtained in (2). Breeding attempts were recorded all year round in both study sites with a minimum peak in September–October, a maximum in March–July, but with active nests in winter too. In terms of the sterility activity of the drug, the results showed only a partial inhibition of reproduction of pigeons fed $\sim 38\text{--}82\text{ mg nicarbazin day}^{-1}$ ($\text{kg bodyweight}^{-1}$ (500 and 800 ppm in feed), which, according to the simulations, would produce only a fleeting reduction of their abundance in the field. Data do not seem to support the use of this drug as an effective control method for feral pigeons, and they cast doubts on the opportunity to make use of chemosterilants, which produce only partial and reversible effects. The use of this drug could perhaps be considered only as part of an integrated pest-management program, which necessarily has to include the reduction of carrying capacity of the urban environment.

Introduction

The rock dove (*Columba livia* Gmelin, 1789), a polytypic species widely distributed across the Old World (Goodwin 1970; Cramp 1985), has a long history of relationship with man, being one of the first tamed bird species (Sossinka 1982). Feral pigeons, which should probably be regarded as an ancient feature of human settlements, originated from domesticated breeds and, at least partially, from synanthropic rock doves (Johnston and Janiga 1995). While detailed information on the historical trend of the abundance of these birds is available for only a limited number of cities, several papers indicate that the number of feral pigeons significantly increased during the second half of the 20th century, both in Europe and in North America (Johnston and Janiga 1995). This trend is frequently associated with an increase in the conflict between man and feral pigeons over the drawing of food from agricultural areas, damage to urban architecture, and the possible transmission of infectious diseases and parasites deriving from breeding sites (see e.g. Bassi and Chiatante 1976; Saini and Toor 1991; Johnston and Janiga 1995; Haag-Wackernagel and Moch 2004; Haag-Wackernagel 2005, 2006). This explains the growing interest in the control of pigeon populations and, in turn, has given rise to the development of several techniques, though the effectiveness of some has not been thoroughly tested (see Johnston and Janiga

1995 for a review). Although it is evident that an effective and long-lasting control of these populations can be obtained by reducing the availability of food and of nesting and roosting sites (see e.g. Haag-Wackernagel 1995, 2002), some alternative techniques could be considered under special circumstances or be used in parallel with the former methods. Among these, pharmacological sterilisation represents a promising technique, both because it gives rise to vital and sterile competitors, which tends to reduce the rate of immigration of pigeons from neighbouring areas, and also because it is often considered an ethically acceptable control method. Until now, various chemosterilants have been tested (see Elder 1964; Sturtevant 1970; Johnston and Janiga 1995 and references therein), but the results obtained in various field and laboratory trials have often been contradictory, suggesting the need for further research.

In order to provide additional information on the possible use of chemosterilisation in pigeon control protocols, taking into account the reproductive output of real feral pigeon populations:

1. We described and quantified the reproductive activity of feral pigeons in two Italian cities, namely Venice and Lucca. In fact, reproductive biology of feral pigeons has been studied by many authors both in North America (e.g. Erskine 1976; Johnston 1984) and in Europe (e.g. Goodwin 1960; Häkkinen

- et al.* 1973; Hetmański 2004; see also Johnston and Janiga 1995 and references therein), but data regarding Italy and, more generally, the Mediterranean basin are substantially lacking.
- We tested the efficacy of nicarbazin on groups of paired feral pigeons maintained in open aviaries. This equimolar complex of 4,4'-dinitrocarbanilide and 4,6-dimethyl-2-pyrimidinol is an anticoccidial drug with rapid (from the 10th day after administration) and reversible side effects on the reproductive performance of laying hens (i.e. spotting and mottling of yolk, reduction of hatchability, reduction of egg production, visible loss of colour in brown-shelled eggs and, in some cases, decreasing egg weight). Those effects are already evident at lower dosages (Hurwitz *et al.* 1975; Reece *et al.* 1985; Jones *et al.* 1990a, 1990b; Hughes *et al.* 1991). Even though the molecular mechanisms by which nicarbazin affects reproduction have not been completely clarified *in vivo*, its negative effects on egg hatchability seem to be due to the degeneration of the vitelline membrane, which becomes more permeable thereby allowing yolk and albumen to mix together (egg yolk mottling) (Cunningham 1976, 1977; Yoder *et al.* 2006b, 2006c). These contraceptive effects have been investigated in order to develop chemical aids to control waterfowl populations (Bynum *et al.* 2005, 2007; Yoder *et al.* 2006c). Notwithstanding some negative notes about the antireproductive efficacy of nicarbazin on pigeons (Elder 1964), the recent testing of this drug in Italy, both on captive and free-living pigeons, produced interesting and encouraging results (Martelli *et al.* 1993; Ferraresi *et al.* 1998, 2000; Bursi *et al.* 2001; see also Yoder *et al.* 2006a).
 - We simulated the possible effects of the use of nicarbazin on a hypothetical feral pigeon population, taking into account the reproductive output recorded for the two above-mentioned cities.

Materials and methods

Reproductive activity

Analyses presented in this study are from two colonies monitored at different times. A colony, with a total of 44 nests, was monitored in Lucca from April 1996 to May 1997. Nests were made in the cavities of a bell tower at an average height of 15 m. A second colony, under a colonnade at a height of 4 m, was monitored in Venice from April 2004 to March 2005. In this case, 16 nests, on average, were on a shelf-like structure, sheltered from sun and precipitation. At both sites, nesting activity was recorded continuously during the year, following a weekly schedule. Weekly survival rates of nests up to 6 weeks of age were analysed using Kaplan–Meier estimation (Hosmer and Lemeshow 1999). Statistical calculations were performed using software R 2.2.0 (R Development Core Team 2005). In order to ease the comparison with the current literature on feral pigeons (Johnston and Janiga 1995) we also calculated global rates of hatching and fledging of laid eggs, even though these parameters could be biased by the lack of independence of the outcome of eggs and nestlings belonging to the same nest.

In order to collect some data on the influence of breeding activity on the population structure, weekly counts were conducted from May 2004 to February 2005 at three sites (small squares or 'campi') in Venice. Pigeons were attracted by distributing food, and the proportion of juveniles (less than 2–3 months old) was determined, basically using plumage and other morphological characteristics such as iris and leg colour to distinguish different age classes (Johnston and Janiga 1995). For the analysis, weekly counts were pooled across sites and then averaged across months.

Experimental trials

Feral pigeons were captured in Venice, sexed by laparoscopy, individually marked with coloured rings and kept captive in aviaries (5 × 3 × 3 m) open along their entire south side during all seasons. Captive pigeons were cared for in accordance with the Guide for the Care and Use of Laboratory Animals (National Academy of Science 1996). Birds were randomly paired and tested for fertility before the experiments. No pair of pigeons was used in tests until it had proved to be fertile by producing at least two consecutive and regularly hatched clutches. Tests were carried out on randomly sorted groups of paired individuals (not on single pairs of pigeons) to simulate the conditions of a breeding colony of free-living pigeons. Water, food and grit (containing a variety of gravel, charcoal, seashell and minerals) were provided *ad libitum*, with the exception of Test A (see below).

Considering the minimum effective doses reported in literature (50–400 ppm in laboratory tests: Martelli *et al.* 1993; 800 ppm in field trials: Ferraresi *et al.* 1998, 2000; Bursi *et al.* 2001), we tested two concentrations of nicarbazin (500 ppm and 800 ppm) by running two experiments per dose. Two types of experimental food were used:

A. Treated maize (Ovistop[®], ACME s.r.l., Cavriago, Reggio Emilia, Italy), covered with the active principle (800 ppm) and with a hydrorepellent film, at dose of 300 g day⁻¹, which corresponded to ~38 mg nicarbazin day⁻¹ kg⁻¹, given an average pigeon bodyweight of ~320 g (see below), integrated with a complete bird-seed (200 g day⁻¹), administered daily for about six months to experimental Group N1 (*n* = 10 pairs) in accordance with the instructions provided by the manufacturer. Control birds (C1, *n* = 10 pairs) were fed with 300 g day⁻¹ of non-treated maize (similar in size to maize Ovistop[®]), mixed with 200 g day⁻¹ of a complete bird-seed. This food regime (25 g day⁻¹ pigeon⁻¹), partially reduced compared with the normal food consumption of captive feral pigeons (~30 g day⁻¹ pigeon⁻¹ according to Murton *et al.* 1972; see also below), was chosen partially to overcome the lack of attractiveness of treated maize, as evidenced by the food residues in the loft of N1-birds (no significant food residues were detected in the control aviary). This regime forced birds to ingest treated maize, even though their food intake was lower than the dose recommended by the manufacturer (15 g day⁻¹ pigeon⁻¹). It is important to note that, at the end of the experiment, this reduced food provision caused a noticeable weight loss both for control (mean bodyweight ± s.d.: C1 (pre-experiment) = 321.1 ± 27.7 g; C1 (post-experiment) = 310.1 ± 23.0 g) and treated

animals (N1 (pre-experiment) = 322.1 ± 32.7 g; N1 (post-experiment) = 292.1 ± 32.9 g).

- B. Bird-seed, in pellets, containing two different concentrations of nicarbazin (500 and 800 ppm) administered daily (*ad libitum*) for about six months. Groups ($n = 8$ pairs per group) were: N2, 500 ppm; N3, 500 ppm; N4, 800 ppm. Control groups (C2, C3, C4; $n = 8$ pairs per group) were fed *ad libitum* with a non-treated bird-seed identical to that fed to treated birds. Given the total food consumption registered in the three trials, which leads to an estimate of ~ 32 g pellet day⁻¹ pigeon⁻¹ with no appreciable intertrial differences, we estimate that the two treatments corresponded to a nicarbazin intake of ~ 52 mg day⁻¹ kg⁻¹ bodyweight (500 ppm) and ~ 82 mg day⁻¹ kg⁻¹ (800 ppm). In N2/C2 and N3/C3, the same two groups of 16 birds were used, but the experimental group of the first trial (N2) was used as control group in the second (C3). The time lag between these two experiments was two months, during which all the pigeons were fed identically with non-treated food provided *ad libitum*. Birds belonging to the N4/C4 groups had never been tested before.

Nest sites were checked weekly. During each visit the number of new nests was noted and marked with a unique colour combination of adhesive tape. Each nest was followed until hatching or until after the eggs had proved to be infertile (eggs not incubated, incubation period longer than the maximum reported for feral pigeons – about three weeks after the deposition of the second egg; see Johnston and Janiga 1995). Nests for which the outcome was not possible to determine, owing to the breakage or the disappearance of the eggs between two consecutive visits, were not considered in the analyses. To take advantage of the breeding potential of feral pigeons in terms of replacement clutches (see Johnston and Janiga 1995), newly hatched chicks were removed during the first week of life and then killed according to the current Italian laws on animal welfare. The experiments were approved by the Animal Care Review Committee of the University of Pisa (*Comitato di Ateneo per la sperimentazione animale*).

Population model

The possible effects of the use of nicarbazin on feral pigeon populations were simulated by means of a population viability analysis conducted using VORTEX 9.50 software (Lacy *et al.* 2005). Given the relative scarcity of available data, the aim of this simulation was not to provide a precise demographic forecast of a given pigeon population subjected to pest control. Instead, it was to discuss the appropriateness of using nicarbazin as a control method for feral pigeons, given the results we obtained in laboratory tests. The values used as initial input for simulations are reported in Table 1 and some of them are discussed below. Simulations were repeated 100 times over a time span of 10 years.

General description

Information on (natal) dispersal of feral pigeons is largely inadequate. Indeed, while it is evident that a significant rate of exchange occurs among colonies within a given city, there are, in practice, no data about the rate of exchange among cities (see Johnston and Janiga 1995), even though it seems

Table 1. Summary of the input parameters used in the simulations

Variable	Value (s.d. ^A)
Demographic closure	Yes
Inbreeding	0 lethals
Concordance of environmental variation of reproduction and survival	No
Catastrophes	0
Mortality at Age 0	43 (4.3)
Mortality at Age 1	34 (3.4)
Breeding system	Long-term monogamy
Age of first breeding	1
Maximum age of reproduction	7
Sex ratio at birth	0.5
Reproductive rates (number of fledglings \pm s.d.)	3.0 ± 1.4
Density dependence	Yes
Percentage breeding ^B	42 (4.2)
$P(0)$	90
B	1, 2, 4
Percentage of males in the breeding pool	95
Initial population size	5000
Start at stable age distribution	Yes
Carrying capacity (K)	5000 (500)

^AStandard deviation of environmental variations.

^BSee text for explanations.

likely that this rate should be relatively low, especially for non-neighbouring cities. In fact, the data at hand indicate that: (1) distances covered by feral pigeons outside the city limits are quite short (usually less than 10 km: Rose *et al.* 2006), and (2) juveniles have rather poor return rates even at relatively short displacement distances (Edrich and Keeton 1977), which might suggest that shorter natal dispersal distances are characteristic of feral populations (Johnston and Janiga 1995). Given the above consideration, the simulated population was assumed to be demographically closed. In order to simplify calculations, we did not model any effect of inbreeding depression, since its influence on the demographic trend is relevant only at low population size (Miller and Lacy 2005). Moreover, we assumed no correlation between environmental variation of reproduction and mortality. Nor did we, in order to evaluate the effects of the chemosterilant under standard conditions, model any catastrophic event during pest control. In the simulations, extinction was defined as the absence of at least one sex.

Mortality

Since there are no published estimates of the annual survival rate of any Italian pigeon population, we used the data reported by Murton *et al.* (1972), regarding feral pigeons breeding on Sandford Docks in Manchester. In that study, the survival rate of juveniles referred to the first six months of life, which could be an underestimate of the true annual survival rate. It is interesting to note, however, that this estimate is quite consistent with the life cycle of pigeons breeding in Basel, reported by Haag (1990), and thus it seems reasonable to think that the bias introduced using this estimate was negligible. We assumed no differences between male and females in mortality rates. Since the literature does not report any estimate of the environmental variability, we artificially set this parameter at 10%. In order to simplify calculations, mortality rate was considered density-independent,

although some data regarding American populations indicate an increased survival of pigeons following an experimentally induced decrease in population density (Kautz and Malecki 1991). Obviously, this choice increased the theoretical effect of the simulated pest control because it reduced the recovery potential of the modelled population when density was low, and the reduced competition among individuals also influenced their mortality rate (see Newton 1998).

Reproduction

According to the available data (Johnston and Janiga 1995) pigeons are monogamous and we assumed long-term fidelity between partners. The age of first reproduction for males and females was set at 1 year, because feral pigeons become fertile when six months old (Johnston and Janiga 1995), although one-year-old birds usually represent a small fraction of the breeding segment of the population (~6%: Johnston and Johnson 1990; Johnston and Janiga 1995; Hetmański 2004; but see Murton *et al.* 1974), and their breeding success is usually low (~80% lower than that of the adults: Johnston and Johnson 1990; Johnston and Janiga 1995; but see Murton *et al.* 1974). According to the life table reported in Haag (1990), the maximum age of reproduction was set at 7 years. This excluded from the simulation any decrease of productivity owing to senescence, which, at least in domestic pigeons, begins at about the age of 7 years (Levi 1974; Johnston and Janiga 1995). The sex ratio at birth was set at 0.5 (Johnston and Janiga (1995)).

Reproductive rate, expressed as the number of fledglings per female per year, was randomly selected for each breeding female by sampling from a normal distribution with mean = 3.0 and s.d. = 1.4, i.e. the parameters derived from the Lucca population considering all nesting sites that produced at least 1 fledgling during the year. We used Lucca data because of the large size of the available sample, but it should be noted that the value recorded for Venice was comparable (3.1 ± 1.6), and both these rates fitted well within the range of the reproductive productivity of feral pigeons recorded both in Europe and in the United States (see Johnston and Janiga 1995).

Reproduction of feral pigeons is density dependent, being high at low density and low at higher density (Haag 1987, 1988, 1991; Kautz and Malecki 1991; Johnston and Janiga 1995). We modelled density dependence by varying the percentage of breeding females in the population according to the equation (Fowler 1981; Miller and Lacy 2005):

$$P(N) = P(0) - [(P(0) - P(K))(N/K)^B], \quad (1)$$

where $P(N)$, $P(K)$ and $P(0)$, are the percentage of females that breed when the population size is N , at carrying capacity (K), and at extremely low density (near 0), respectively, while the exponent B is a constant that determines the form of the curve. For example, if $B=1$, the percentage of females that breed changes linearly with population size, whereas if $B=2$, this percentage is a quadratic function of population size (see Fig. 1). Given the high mobility of feral pigeons, we ignored any possible Allee effect (Allee *et al.* 1949), i.e. the decrease in the proportion of females breeding at low densities possibly because of difficulty in finding mates. The parameters of this equation were set as follows. In the absence of precise estimates, $P(0)$ was set at 90%, because of both the

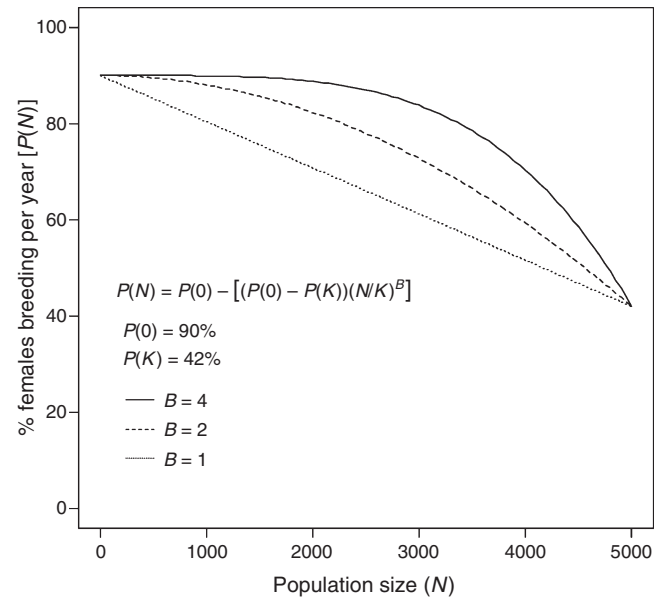


Fig. 1. Relationship between the percentage of breeding females and population size for the parameters $P(0)$, $P(K)$ and B used in the simulations.

high breeding potential of feral pigeons, due, at least in part, to their domestic origin (Johnston and Janiga 1995) and the considerable increase in productivity that follows a decrease in population density (see, for example, Haag 1991). The effect of B on the simulation was explored by considering three different values of this parameter (1, 2, 4), which correspond to the curves reported in Fig. 1. Regarding $P(K)$, we assumed that most of the current populations of feral pigeons have reached the limit of the carrying capacity of the urban environment, owing to their high breeding potential and to the relative stability of this habitat. This assumption is further supported by the following considerations:

1. As mentioned in the Introduction, the size of most feral pigeon populations substantially increased during the middle of the last century (1940–1970), following changes in agricultural practices and the human demographic explosion after World War II (Johnston and Janiga 1995).
2. The available data indicate that feral pigeons are characterised by a high intrinsic demographic rate of increase (Neal 2004), particularly considering the rapid recoveries of populations subjected to considerable harvesting during pest-control activities (see Kautz and Malecki 1991; Sol and Senar 1992; Johnston and Janiga 1995) or after catastrophic events such as World War II (see Johnston and Janiga 1995). This demographic characteristic should lead pigeon populations to rapidly saturate the capacity of the urban environment.
3. Periodic censuses performed during the last decades of the 20th century in a small number of cities (e.g. Barcelona, Bratislava) revealed a noticeable intra-annual, but a very low inter-annual variability of counts of resident pigeons, thus indicating a substantial stability of these populations (see Johnston and Janiga 1995). This low inter-annual variability was confirmed by four annual, late-autumn

quadrat counts (see Senar 1996) carried out in Venice during 2000–04 on 213 randomly selected 6-ha sampling units (Fig. 2).

Following this assumption, we chose by trial and error the value of $P(K)$ as that determined a fundamental stability of the population as defined by the demographic parameters listed in Table 1. However, this was in the absence of density-dependent reproduction and with a carrying capacity much higher than the initial population size (10 000 birds). The value calculated using this protocol was 42% [deterministic intrinsic rate of increase = -0.001 ; mean growth rate (20 years, 100 iterations) = -0.0053 (0.0016 s.e.)], which compares reasonably well with the values suggested in the literature that range between 20% and 40% of the population size (Murton *et al.* 1972; Johnston and Janiga 1995). The environmental variability of this parameter was artificially set at 10% of its value. A large proportion (95%) of adult males were considered to make up the pool of available breeders as suggested by the considerable increase in courtship displays directed to mated females experimentally deprived of their mates (Lovell-Mansbridge and Birkhead 1998).

Population

To simplify calculations, we modelled a single population of 5000 pigeons, which roughly corresponds to the population abundance of pigeons in Lucca (Bechelli 1998). It was assumed that this population started at the stable age distribution. As previously specified, the carrying capacity (K) was assumed to be identical to the initial population size, with no trend during the simulation period, and its environmental variability was artificially set at 10% of K .

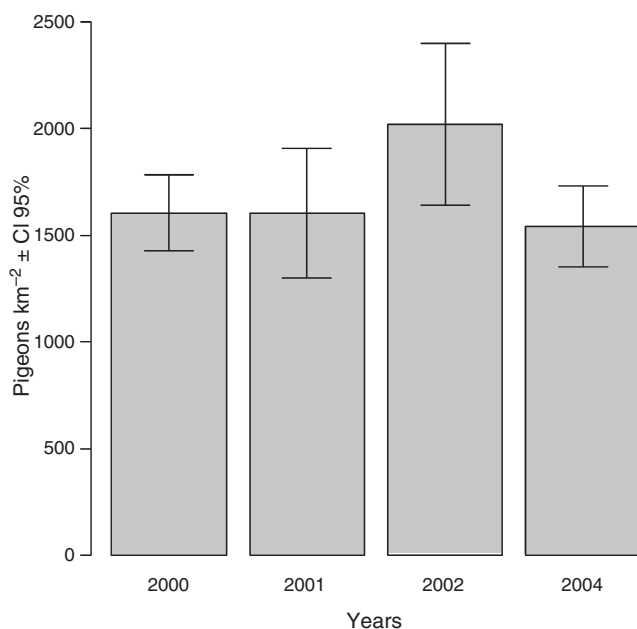


Fig. 2. Uncorrected mean density (pigeons $\text{km}^{-2} \pm 95\%$ confidence intervals) recorded in Venice in late autumn quadrat counts ($n = 213$ 6-ha randomly selected sampling units). Note that data for 2003 are lacking.

Pest control

A series of simple simulations was performed to investigate the effects of the reduction of fertility on the above-mentioned three populations (one for each value of B , see Fig. 1). Population trends were simulated for a five-year period of pest control followed by five years of recovery, during which pest control was stopped and fertility returned to its initial value. We considered three different scenarios: 50%, 70% and 90% fertility reduction. The lowest level (50%) roughly corresponded to the maximum reduction of the total number of hatchlings compared with controls observed during our experimental trials on nicarbazin (see Results). The other two levels were included in order to explore other hypothetical scenarios arising from the use of more effective but still short-lasting contraceptives (e.g. higher doses of nicarbazin: Yoder *et al.* 2006a). We assumed that the sterility agent was administered to the pigeons daily, and that all the pigeons within the considered populations were treated during the five years of control. We thus regarded the presented results as the maximum theoretical effect of chemosterilisation on our simulated populations.

Results

Reproductive activity

As reported in Fig. 3a, which shows the percentage of active nests out of the total number of monitored breeding sites, breeding occurred throughout the year, with minima in autumn–winter in both cities. It is interesting to note that small proportions of pigeons were actively reproducing in winter also, when temperatures as low as -5°C were recorded both in Lucca and Venice. In both cities, the period of most intense reproductive activity was March–July, when we recorded an average of 70% and 50% of occupied nests in Venice and Lucca, respectively. The number of breeding attempts per nesting site was comparable

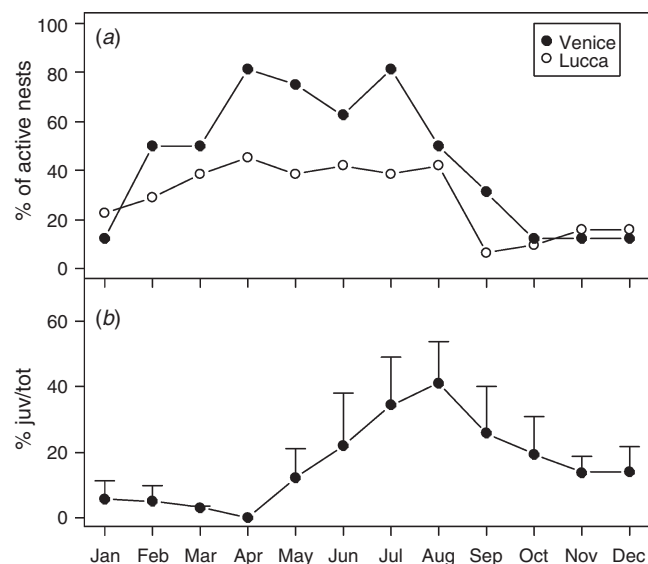


Fig. 3. (a) Monthly percentage of active nests out of the total number of nests monitored. (b) Percentage of juvenile birds recorded in three different sites in Venice (mean \pm s.d.); mean number of considered birds per month (minimum–maximum) = 11–120.

between the two cities [median (interquartile range, range): Venice = 4 (4–6, 1–7), Lucca = 4 (2–6, 1–7)].

Information on hatching and fledging rates is presented in Fig. 4, which reports the weekly survival rate of monitored nests, and in Table 2, which reports the global rates of hatching and fledging in reference to the number of eggs laid. On the whole, the annual rates observed in the two cities were relatively comparable and indicated that more than half of all the breeding attempts produced at least one fledgling. Considering the two periods separately, it is interesting to note that nest survival in Venice and Lucca was substantially similar during spring–summer (0.55 versus 0.56), while in autumn–winter survival in Venice was rather lower than that recorded in Lucca

(0.33 versus 0.81), though the Venice estimate was based on a small sample size.

The annual pattern of reproductive activity and breeding success was at least partially mirrored in the proportion of juvenile birds recorded in the three monitored sites in Venice. As shown in Fig. 3b, the maximum peak occurred in August, when juveniles represented more than 40% of observed pigeons. This proportion then decreased abruptly until April, when almost no juveniles were recorded.

Experimental trials

As reported in Table 3, the effects of nicarbazin at the lower consumption rates (N1/C1, about ~38 mg nicarbazin day⁻¹ kg⁻¹

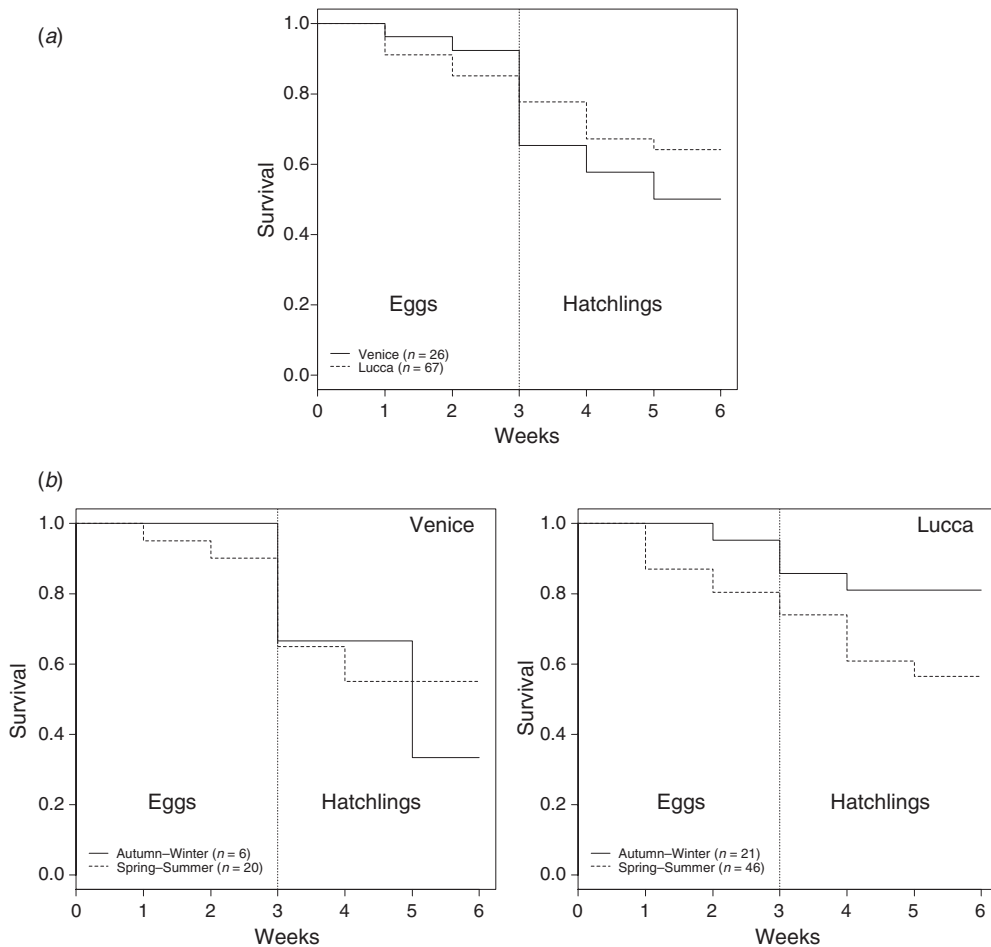


Fig. 4. (a) Annual, and (b) autumn–winter and spring–summer Kaplan–Meier estimates of weekly nest survivals recorded in Venice and Lucca.

Table 2. Rates of hatching and fledging for feral pigeons in Lucca and Venice

	N		% of eggs		% of hatched eggs	
	Lucca	Venice	Lucca	Venice	Lucca	Venice
No. of monitored nests	44	16				
Total no. of laid eggs	196	70				
Hatched	117	47	59.7	67.0		
Fledged	96	37	49.0	53.0	82.0	78.0

Table 3. Breeding output of controls (C1–C4) and experimentals (N1–N4) treated with different doses of nicarbazin
 95% confidence intervals (CI 95%) were calculated using bootstrap with 5000 replications

	N1 (800 ppm)	C1	N2 (500 ppm)	C2	N3 (500 ppm)	C3	N4 (800 ppm)	C4
Food provision	25 g day ⁻¹ pigeon ⁻¹							
Average nicarbazin consumption (mg day ⁻¹ kg ⁻¹ bodyweight)	38		52	<i>Ad libitum</i>	52	<i>Ad libitum</i>	82	<i>Ad libitum</i>
Test duration	160 days (Mar.–Aug.)		154 days (Dec.–Apr.)		148 days (Jul.–Dec.)		193 days (Aug.–Feb.)	
Laid eggs (mean eggs nest ⁻¹)	91 (1.8)	78 (1.9)	27 (1.9)	44 (2.0)	49 (2.0)	50 (1.9)	56 (1.8)	68 (1.8)
% hatched eggs nest ⁻¹	60.8 (49.0–72.6)	86.9 (78.6–97.6)	78.6 (64.3–96.4)	93.2 (86.4–100.0)	84.0 (74.0–96.0)	79.6 (68.5–92.6)	54.8 (38.7–71.0)	89.2 (81.1–98.6)
[mean (CI 95%)]								
Hatchlings nest ⁻¹	1.2 (1.0–1.4)	1.7 (1.5–1.9)	1.6 (1.3–1.9)	1.9 (1.7–2.0)	1.6 (1.4–1.9)	1.5 (1.2–1.7)	1.0 (0.7–1.3)	1.6 (1.5–1.8)
[mean (CI 95%)]								
No. of hatchlings	61	70	22	41	41	40	32	61
% Δ hatchlings (N–C)		-13%		-46%		+2%		-48%

bodyweight; N2/C2 and N3/C3, $\sim 52 \text{ mg day}^{-1} \text{ kg}^{-1}$) were not consistent. The rate of egg production did not follow a regular trend, while hatchability was reduced in two out of three experiments, even though the maximum observed effect was only about -30% (N1: 1.2 hatchlings nest $^{-1}$; C1: 1.7 hatchlings nest $^{-1}$). At the higher consumption rate (N4/C4, $\sim 82 \text{ mg day}^{-1} \text{ kg}^{-1}$) the effects of nicarbazin were slightly increased, even though they did not exceed -40% (N4: 1.0 hatchlings nest $^{-1}$; C4: 1.6 hatchlings nest $^{-1}$). On the whole, in three out of four trials, the recorded reduction of total productivity was noticeable, though rather variable, ranging from 13% (N1/C1) to 48% (N4/C4).

Population model

The results of simulations are reported in Fig. 5. In all the scenarios considered, populations showed a relatively rapid response to the treatment after the first year (about -18% in

the first case, about -27% in the second, and about -41% in the third). Thereafter, the decrease of abundance diminished with time until the last year of treatment in the 50% scenario, while it tended to be relatively constant in the other two. The recovery rate strongly depended on the degree of pest control of the previous five years. In general, in the first two scenarios (50% and 70% reduction of fertility) the populations regained their size at the end of the period in question in all cases except where $B=1$, while the recovery after 90% of fertility reduction is much slower. On the whole, the extent of density dependence of reproduction (the B parameter in Eqn (1), see Materials and methods) influenced the results of the simulations mostly at the lower fertility-reduction levels (50% and 70%).

It is important to note that five years with fertility reduced by 50%, i.e. approximately the maximum effect of nicarbazin recorded in our laboratory trials (see Table 3), produced, at most, a halving of the population at the end of the treatment.

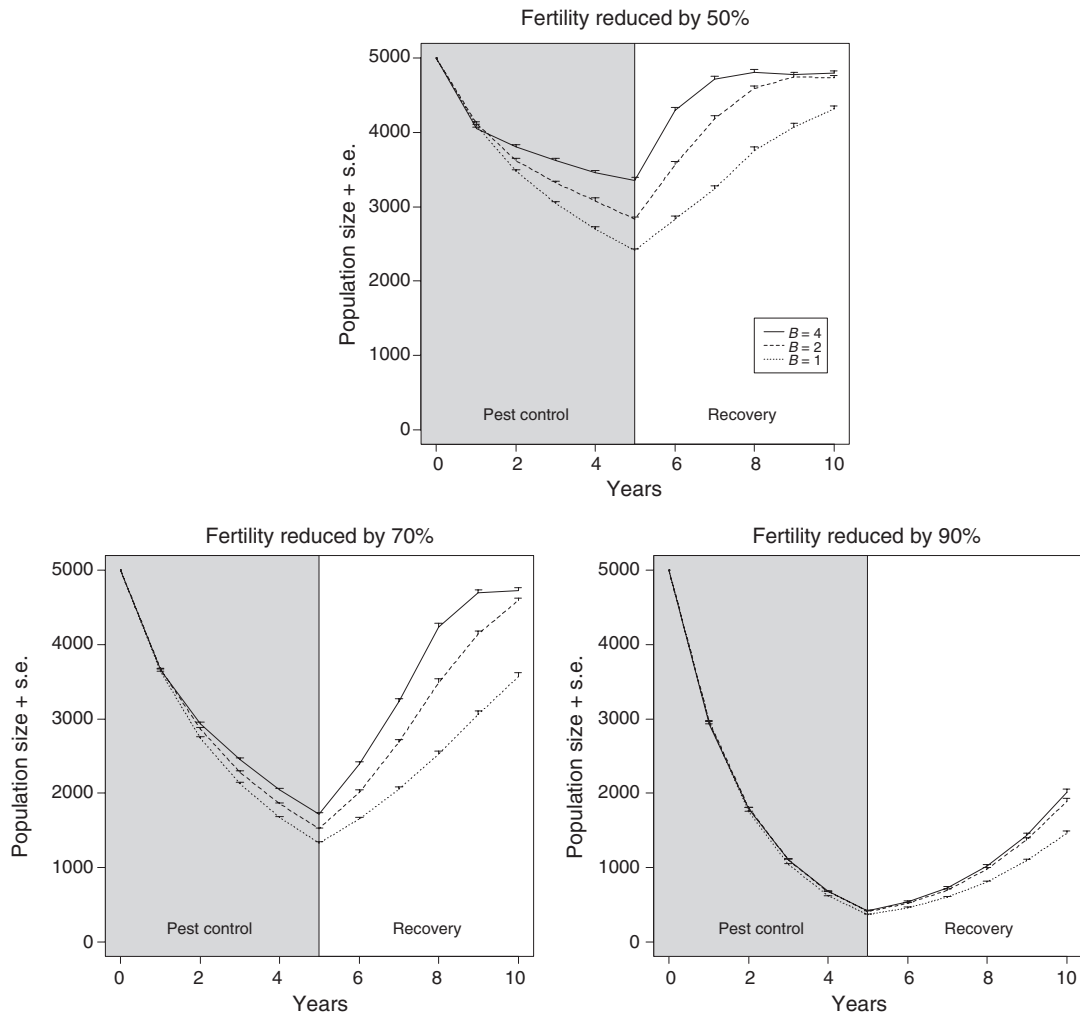


Fig. 5. Feral pigeon population trends predicted by 100 iterations after 5 years of various degrees of fertility control (-50 , -70 , -90%) followed by five years of recovery. Different lines refer to different values of B (see Fig. 1).

Discussion

Reproductive activity

Knowledge of the biology and behaviour of feral pigeons is essential for an understanding of how to control their populations, given (1) the formidable capacity of these birds to become pests by any standards, and (2) the widespread distribution of this species (Lever 1987), which can breed under very different climatic conditions, which, in turn, can profoundly influence their breeding phenology.

In both our case studies, the reproductive period may be considered to last all year long, although pigeons in Lucca and Venice showed a clear peak (higher number of nesting attempts and greater success) from March to the moult period in late summer. This pattern is similar to what has been observed in Bratislava, Prague, Brno, Zagreb and in Kansas (see Johnston and Janiga 1995 and references therein), thus emphasising the extent to which the characteristics of the fluctuations of these two Italian populations fit with others studied in temperate climates. In fact, in a study of pigeon populations, the proportion of birds behaving seasonally in terms of their reproductive period showed a clear geographical variation, with the length of the reproductive period tending to scale inversely to latitude (Johnston and Janiga 1995).

As recorded for the timing of reproduction, also the reproductive productivity was highly comparable between Lucca and Venice and fitted well within the range of the reproductive productivity of feral pigeons recorded both in Europe and in the United States (Johnston and Janiga 1995). The published data, however, reveals significant inter- and intralocality variation, which indicates that the reproductive performance of these birds is clearly dependent on local ecological conditions (e.g. food availability, local climate, etc.: Haag 1985, 1987; Johnston and Janiga 1995). In this regard it should be noted that the proportion of winter fledglings differed between the two cities. Indeed, while in Venice only 11% of the total number of juveniles produced during the year fledged in winter, in Lucca this rate increased to 41%. It is likely that this discrepancy reflected differences in the microclimatic characteristics of the two cities and in the availability of food resources. In fact, in terms of climatic conditions, Venice is located on the north-east coast of Italy and thus experiences lower winter temperatures than those in Lucca [average minimum and maximum temperatures in January: Venice = $-0.9/+5.8^{\circ}\text{C}$ (period: 1961–1990; source: Servizio meteorologico dell'Arma Aeronautica Militare Italiana, <http://www.meteoam.it>); Lucca = $+1.8/+11.8^{\circ}\text{C}$ (period: 1960–1987, 1991–1998; source: La.M.M.A., Regione Toscana, <http://www.lamma.rete.toscana.it/ita/climanew/capoluoghi/lucca.html>)]. Regarding the availability of trophic resources, it is interesting to note that Lucca pigeons could take advantage of a highly predictable food resource (cereal-processing mills) all year long located quite close to the city (see Soldatini *et al.* 2006). This pattern of food availability associated with the relatively mild temperatures could explain the relatively higher survival rates observed in Lucca, especially during autumn–winter. On the other hand, Venice pigeons experience rather different conditions during spring–summer and autumn–winter.

Indeed, the impressive tourist traffic in Venice (~4 million tourists in 2003: COSES 2004), especially high during the spring and summer periods, means a very great availability of food within the city during these months, thus allowing a high fledgling success, even under the extreme population density characteristic of Venice (see Soldatini *et al.* 2006 for other details). On the other hand, the marked reduction in tourist traffic during winter, possibly exacerbated by the substantial decrease of temperatures, probably explains both the low number of breeding attempts and their limited success, especially if compared to what was recorded in Lucca.

Apart from these ecological considerations, it is important to note that the intensity of breeding output during cold months could profoundly affect the outcome of any pest-control protocol designed principally to reduce the maximum peak of productivity recorded in spring–summer. This is relevant to the use of a sterility agent such as nicarbazin, whose effects are completely and rapidly reversible. Indeed, while in Venice-like situations pigeon-control operations could be concentrated in spring–summer only, in Lucca-like situations the distribution of the chemosterilant should probably be extended over the whole year in order to obtain significant and long-lasting results.

Experimental trials

Contrary to expectations, the recorded effects of nicarbazin were relatively modest and also variable across the different trials. It should be noted that our experimental protocol (i.e. the use of non-homogeneous strains of pigeons breeding in groups) did not allow a proper control of several variables, such as individual susceptibility to the treatment, the daily consumption rate of the chemosterilant, etc., which are probably the main causes of the significant variability of our experimental outcomes. However, our aim was not to accurately estimate the effect of nicarbazin on individual pairs of birds, but to simulate its global effect on productivity in groups of feral pigeons, not limited by food or availability of nesting sites.

Contrary to the data reported on laying hens (see, for example Jones *et al.* 1990b; Johnston *et al.* 2002), but in line with the results obtained on captive pigeons (Martelli *et al.* 1993; see also Yoder *et al.* 2006a), this chemosterilant had a limited effect on the rate of egg-laying at tested doses. On the other hand, we observed a noticeable dosage-dependent effect of nicarbazin on egg hatchability. At an average consumption of $\sim 52 \text{ mg day}^{-1} \text{ kg}^{-1}$ bodyweight (500 ppm in feed; N2/C2, N3/C3), the effect on the hatching rate was inconsistent across the two trials, and not comparable to the results of Martelli *et al.* (1993), who reported a substantial zeroing of this rate in homing pigeons fed daily *ad libitum* with bird-seed in pellets mixed with 400 ppm of chemosterilant. On the other hand, at $\sim 82 \text{ mg day}^{-1} \text{ kg}^{-1}$ (800 ppm in feed; N4/C4) we recorded a lowering of hatching rate ($\sim 40\%$), which was, however, far below the 100% reduction reported by Martelli *et al.* (1993). Because of the apparently unattractive nature of the treated maize, which evidently led to reduced ingestion of the chemosterilant and weight loss in treated birds (see Materials and methods), the results of the trial N1/C1 should be considered with care. Indeed, notwithstanding the low nicarbazin consumption, the reduction of hatchability was only $\sim 10\%$ lower than that recorded for N4/C4. In this regard

it should be noted that: (1) at least in mallards, the pelleted feed caused a reduced absorption of 4,4'-dinitrocarbanilide, the active anticoccidial component of nicarbazin, with respect to coated corn (Yoder *et al.* 2006d); and (2) food shortage has negative effects on productivity in several bird species (see Martin 1987; Newton 1998).

Even though the maize Ovistop[®] had been previously used in the field to control Italian feral pigeon populations (see Bursi *et al.* 2001), our evidence clearly suggested the possibility of serious technical problems arising during pest-control operations using this product because of its lack of attractiveness. Indeed, as reported in several papers (Sol *et al.* 1998, 2000), competition for food is intense in feral pigeons, especially when pigeons foraged on food provided by the public. This determines a substantial asymmetry in the distribution of birds over feeding sites, with more effective competitors (usually adult birds) consistently found more often than expected in the most rewarding feeding site, and less effective competitors (usually juveniles) more often found in suboptimal and less preferred sites (Sol *et al.* 2000). It could thus be predicted that when more attractive food resources are available, treated maize would be mainly consumed by poorer competitors, which probably do not belong to the breeding segment of the population; this would substantially reduce the potential effect of the pest-control operation. In this regard it is interesting to mention the data of Dell'Omo *et al.* (1998), which reported a low return rate of pigeons (~50%) to a feeding site supplied with nicarbazin-treated food. Given the available data, we can only speculate about why Ovistop[®] was not well accepted by the pigeons. The regular food consumption by controls clearly indicates that corn size was unimportant. We suspected that the hydrorepellent external film, which was 'rubbery' to touch, makes the treated maize less attractive. While mainly speculative, this hypothesis should be considered when preparing commercial contraceptive baits.

To sum up, the outcome of our experiments do not fit the evidence reported in the literature on nicarbazin (Martelli *et al.* 1993; Ferraresi *et al.* 1998, 2000; Bursi *et al.* 2001), which indicated a significant reduction of fertility even in pigeons fed *ad libitum* with 50 ppm nicarbazin-treated feed (about -67%), although our results do not confirm the absence of any antireproductive activity of this chemical as reported by Elder (1964). It should be noted, however, that Elder (1964) tested pigeons for a short period only and used treatment concentrations (0.01% and 0.1% of nicarbazin in the diet) that proved to be highly toxic. While proving the absence of any toxic effect of the drug at tested doses (data not reported; see Sbragia 2000), our results indicated only a relatively small effect on the reproductive rate of pigeons, not in the least comparable to the complete cessation of reproduction in birds fed *ad libitum* with 400 ppm nicarbazin-treated feed (roughly 40 mg day⁻¹ kg⁻¹ given that average homing pigeons weigh 475 g and eat ~10% of their bodyweight: see Schrag 1974) reported in Martelli *et al.* (1993). Given the available evidence, it seems difficult to ascertain the reasons for this inconsistency. The different protocol (e.g. the different strain of pigeons used: domestic (homing) versus feral) should certainly be taken into consideration, but it should be noted that recent tests indicate the need of a much higher dose (5000 ppm) in order to obtain a reduction of ~60% in

egg hatchability in pigeons (Yoder *et al.* 2006a). These results suggest that, as recorded for mallard and geese (Yoder *et al.* 2005), the degree of uptake of nicarbazin in pigeons is much lower than that recorded for chickens, thus giving further support to our experimental evidence.

Population model

Our simulations clearly show that even under the most favourable conditions for pest control (low density dependence of reproduction) the population decrease obtained at the end of the five years of fertility reduced by 50% (i.e. approximately the maximum effect of nicarbazin recorded in our laboratory trials) was not particularly remarkable. This negative evaluation is further supported by considering (1) the rapid loss of the effects achieved after the withdrawal of the compound from the diet, and (2) that, as previously suggested in the 'Materials and methods' section, the results presented should be regarded as the maximum theoretical effects of this chemosterilant on our simulated feral pigeon populations. Indeed, in order to simplify our model, we first completely disregarded any density dependence in survival rate, even though several authors suggest that this phenomenon is not negligible in 'real' populations (see e.g. Johnston and Janiga 1995), as further testified by the substantial ineffectiveness of even massive culling programs (see e.g. Murton *et al.* 1972; Martin and Martin 1982; Kautz and Malecki 1991; Sol and Senar 1992). Second, in order to reproduce 'in the field' the maximum reduction of productivity recorded in the laboratory, where birds were fed *ad libitum* with treated food, we assumed that all the birds consumed an adequate dose of the drug throughout the year. This assumption appears unlikely. Indeed, some feral pigeon populations mostly depend on food resources located within the urban environment (see e.g. Murton *et al.* 1972; Simms 1979; Sol and Senar 1995; Rose *et al.* 2006), while in other cities most birds fly to adjacent agricultural areas for food (see, for example, Havlin 1979; Janiga 1987; Soldatini *et al.* 2006 and references therein), taking advantage of the presence of abundant food resources. In the first case it may be possible to manage food availability in order to induce pigeons to systematically forage on feeding sites supplied with a chemosterilant, even though both theoretical considerations and field data (see e.g. Dell'Omo *et al.* 1998) indicate that this should be extremely difficult. On the other hand, in the second case, it would be extremely difficult to distribute the sterility agent to the entire population, especially considering the relatively low palatability of the commercial drug (see above). In practice, it seems likely that a significant fraction of the population would not be treated with nicarbazin. According to the data reported in Kautz and Malecki (1991), these birds would probably show an increase in reproduction and survival rate as a response to the reduced density caused by the chemosterilant, thus at least partially compensating its effects. It is interesting to note, moreover, that, given the relatively continuous breeding activity observed in Venice and Lucca, limiting the distribution of nicarbazin only to the spring-summer months (i.e. during the peak of the nesting period) in order to limit the cost of pest control, would further reduce the effect on population size by 41%, according to the proportion of winter nesting attempts recorded in Lucca (see Fig. 3a). Third, although we do not have enough data to estimate precisely the relationship between population density and reproduction in real pigeon

populations, it seems reasonable to consider B values greater than 1 as realistic. Indeed, as suggested by Fowler (1981), density dependence in reproductive success can often be modelled with a quadratic function ($B = 2$) and this hypothesis is supported by the data reported in Haag (1991), which showed a quadratic relationship between reproductive success, expressed as eggs and nestling survival, and density of pigeons within two colonies in Basel.

Taking into account all the above considerations, it seems reasonable to regard nicarbazine as a very weak control method for feral pigeon populations. This is a consequence not only of the relatively low effect on productivity recorded in our experimental trials, but also of the likely absence of long-lasting effects, which probably leads to a rapid resumption of breeding activity when the treatment is stopped. In fact, the results obtained in our simulations could have been achieved also by a relatively modest effort aimed at reducing the carrying capacity of the urban environment by an average of $\sim 11\%$ per year, considering the case of $B = 2$. Indeed, as suggested by other authors (e.g. Johnston and Janiga 1995), the elimination of food supply and/or nesting and roosting sites should be regarded as the best way to control pigeon populations, especially because it produces a long-lasting reduction in population size. The recent tests indicating an increased effect (about -60% of egg hatchability) of a much higher dose of nicarbazine (Yoder *et al.* 2006a) do not seem to modify significantly the above-mentioned conclusions. Indeed, as shown by our simulations, only a massive reduction of fertility (90%) has significant and long-lasting effects on the modelled populations, while even a reduction of fertility by 70%, which produces an approximate two-thirds reduction in abundance, could be quite rapidly compensated after 4–5 years. It should be noted that even the 70% scenario appears quite unlikely considering the available estimates of the effects of nicarbazine under the best laboratory conditions.

It follows that our simulated results clearly do not fit the published data, which report a remarkable reduction of the feral pigeon population size (even 60% after the first year of treatment) in several Italian cities following the distribution of nicarbazine (800 ppm) in the field (see Bursi *et al.* 2001). Since it seems reasonable to exclude the possibility that the actual dose received by pigeons in the above-mentioned trials was higher than that received by our N4 group, we could only speculate about several reasons that could at least partially help to explain these contradictions. First of all, like most pest-control studies on feral pigeons, all the studies used biased methods, such as an *ad hoc* and uncalibrated index of abundance as a means of estimating population size trends. This makes it rather difficult to objectively evaluate and quantify the actual effects of the chemosterilant. Second, some of these studies lacked adequate experimental controls and replications, and sometimes covered a very short time span (even less than 1 year: Bursi *et al.* 2001). Bearing in mind the intrinsic variability of pigeon counts (Uribe *et al.* 1984; Senar 1996) this would be quite a serious flaw in these field trials. Third, quite frequently the chemosterilant was distributed at the same time as a significant effort was made to restrict the availability of food resources within the city and, sometimes, even to reduce the number of suitable nesting and roosting sites (see Zucconi *et al.* 2003), with the effect of decreasing the carrying capacity of the urban

environment. Fourth, the consistent reduction of population size recorded in some Italian cities after only 4–8 months of distribution of nicarbazine (see Bursi *et al.* 2001) cannot be easily explained by the effect of a sterility agent alone, even one more effective than nicarbazine. This inconsistency further emphasises the problems related to obtaining an unbiased estimate of the true effect of nicarbazine in field trials and possibly points to the need to consider the effect of other control actions, such as the above-mentioned reduction of carrying capacity, in evaluating the presented results.

On the whole, as previously suggested, the inconsistency between our results and those reported in the literature clearly calls for further investigation both under laboratory conditions and in the field. Nevertheless, it seems reasonable to conclude that our data do not particularly support the use of nicarbazine as a control method for feral pigeon populations. The use of this drug could perhaps be considered, but only as part of a highly structured pest-control protocol, which has to include exclusion, and reduction of availability of food and of nesting sites (see also Haag-Wackernagel 1995, 2002). As indicated by the fast recovery rate of the simulated pigeon population which followed the end of the fertility control, at present only the reduction of carrying capacity of the urban environment is a reasonable way to obtain significant and, above all, long-lasting effects on pigeon populations.

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