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The demography of free-roaming dog populations and applications to disease and population control

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Summary

1. Understanding the demography of domestic dog populations is essential for effective disease control, particularly of canine-mediated rabies. Demographic data are also needed to plan effective population management. However, no study has comprehensively evaluated the contribution of demographic processes (i.e. births, deaths and movement) to variations in dog population size or density, or determined the factors that regulate these processes, including human factors.

2. We report the results of a 3-year cohort study of domestic dogs, which is the first to generate detailed data on the temporal variation of these demographic characteristics. The study was undertaken in two communities in each of Bali, Indonesia and Johannesburg, South Africa, in rabies-endemic areas and where the majority of dogs were free-roaming. None of the four communities had been engaged in any dog population management interventions by local authorities or animal welfare organizations. All identified dogs in the four communities were monitored individually throughout the study.

3. We observed either no population growth or a progressive decline in population size during the study period. There was no clear evidence that population size was regulated through environmental resource constraints. Rather, almost all of the identified dogs were owned and fed regularly by their owners, consistent with population size regulated by human demand. Finally, a substantial fraction of the dogs originated from outside the population, entirely through the translocation of dogs by people, rather than from local births. These findings demonstrate that previously reported growth of dog populations is not a general phenomenon and challenge the widely held view that free-roaming dogs are unowned and form closed populations.

4. *Synthesis and applications*. These observations have broad implications for disease and population control. The accessibility of dogs for vaccination and evaluation through owners and the movement of dogs (some of them infected) by people will determine the viable options for disease control strategies. The impact of human factors on population dynamics will also influence the feasibility of annual vaccination campaigns to control rabies and population control through culling or sterilization. The complex relationship between dogs and people is critically important in the transmission and control of canine-mediated rabies. For effective management, human factors must be considered in the development of disease and population control programmes.

Key-words: demography, developing communities, disease transmission, free-roaming domestic dogs, population management, rabies control, vaccination coverage

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Introduction

Understanding the demography of domestic dog populations in the developing world is critical for planning effective population management and disease control, particularly for rabies which causes around 55,000 human deaths per year (Knobel *et al.* 2005), as well as for other dog-mediated zoonoses prevalent in developing countries (Macpherson, Meslin & Wandeler 2012). Most human rabies cases are caused by bites from dogs infected with this fatal encephalitic disease. Rabies is directly transmitted by bites between dogs and can be readily controlled by canine vaccination (Jackson 2013). Demographic processes (i.e. births, deaths and the movement of dogs into and out of populations) contribute to variations in population size, density, vaccination coverage and disease transmission. A number of studies, encompassing a range of geographical locations, have assessed aspects of canine demography, including longitudinal studies where population management was not systematic (Chomel *et al.* 1987; Kitala *et al.* 2001; Pal 2001; Hampson *et al.* 2009). However, the contributions of demographic processes to population and disease dynamics, and the factors that regulate these processes, have not been comprehensively investigated.

Several studies have estimated variations in the size of dog populations, where most dogs are free-roaming and where there has been no population control (Brooks 1990; Butler & Bingham 2000; Kitala *et al.* 2001; Pal 2001; Hampson *et al.* 2009; Acosta-Jamett *et al.* 2010; Gsell *et al.* 2012). These all report population growth; but with the exception of Pal (2001), growth was determined indirectly from estimates of births and deaths and age structure in a subset of dogs or extrapolated from human census data and dog to human ratios. Rapid declines in vaccination coverage, necessitating at least annual vaccination campaigns, were also determined from similar data (Brooks 1990; Kitala *et al.* 2001; Hampson *et al.* 2009; Acosta-Jamett *et al.* 2010; Gsell *et al.* 2012). The effect of movement on these variations was not considered.

There is increasing evidence that most free-roaming dogs are owned (Cleaveland & Dye 1995; Butler & Bingham 2000; Windiyaningsih *et al.* 2004; Gsell *et al.* 2012). Movement of dogs by people may therefore contribute to population dynamics (Chomel *et al.* 1987; Beran & Frith 1988), the spread of rabies (Denduangboripant *et al.* 2005; Zinsstag *et al.* 2009; Talbi *et al.* 2010; Townsend *et al.* 2013) and offset the impact of population control programmes that aim to reduce population density through culling (Beran & Frith 1988; Windiyaningsih *et al.* 2004) or sterilization (Totton *et al.* 2010).

In canine epidemiological and ecological models, it is often implicitly assumed that free-roaming dog populations are regulated through environmental resource constraints on births and deaths (Kitala *et al.* 2002; Hampson *et al.* 2007; Zinsstag *et al.* 2009; Totton *et al.* 2010). This has been described in rabies control policy by the logistic growth model (Wandeler 1985; WHO & WSPA 1990); a simple model that assumes all individuals have equal access to resources at the population level and births and deaths vary linearly and uniformly with population density, a surrogate for environmental resource availability (Sibly & Hone 2002; Vandermeer & Goldberg 2003). While the overall contribution of resource availability to variations in vital rates is controversial, empirical evidence suggests that it is important in a range of feral ungulate and wildlife populations (Choquenot 1991; Albon *et al.* 2000; Coulson, Milner-Gulland & Clutton-Brock 2000; Coulson *et al.* 2001, 2004; Bonenfant *et al.* 2002). The relationship between density and births and deaths is demonstrable in these populations because of large fluctuations in population density about a carrying capacity, K. These fluctuations are either intrinsic or the result of deliberate perturbations, such as harvesting. Simple models assume that as populations approach or exceed K, all individuals in the population uniformly experience the effects of resource depletion. In reality, the relationship between density and births and deaths is complex and may be nonlinear with greatest change in births and deaths at or near K (Fowler 1981), and resource depletion primarily affecting those individuals with the highest nutritional requirements, for example, the survival of rapidly growing juveniles (Clutton-Brock, Major & Guinness 1985; Coulson *et al.* 2001; Bonenfant *et al.* 2002).

The assumption that environmental resource constraints regulate dog populations has never been properly investigated. In accordance with the logistic growth model, it implies the primary food source of free-roaming dog populations is available to all dogs and most likely to be environmental refuse and that dog populations are self-sustaining and population size, and vital rates are self-regulating; effectively, the dogs are unowned. This contradicts increasing evidence that most free-roaming dogs are owned (Cleaveland & Dye 1995; Butler & Bingham 2000; Windiyaningsih *et al.* 2004; Gsell *et al.* 2012) with serious implications for disease and population control measures and for animal welfare. However, determining the relationship between dog population density and births and deaths is hampered by the lack of longitudinal data from dog populations with substantial variations in density. Although dog populations are frequently culled, culls are often nonsystematic and difficult to monitor, which complicates assessment of the role of environmental resource constraints in regulating free-roaming dog populations. Furthermore, similar to ecological studies of feral ungulates and wildlife, quantifying variations in the distribution, volume, nutritional content and, more critically, uptake of environmental resources is generally not practicable. However, the unique relationship between dogs and humans affords a multifaceted approach, combining community-based methods with direct observations to infer the mode of ownership and food sources for individuals.

Using this multifaceted approach, we directly measured temporal variations in population size and the contributions of births, deaths and human-mediated movement on these variations. We also investigated the effect of human and other factors, including environmental resource constraints, associated with these demographic processes. To facilitate comparisons between different environments and cultures, two populations of free-roaming dogs were selected in Bali, Indonesia, and two in Gauteng Province, South Africa, where rabies is endemic and where free-roaming dogs have been assumed to be unowned. We found constant or declining population sizes with no clear evidence of population regulation by environmental resource constraints; that almost all identified dogs in the communities were owned and fed regularly by their owners, consistent with population size regulated by human demand; that a substantial fraction of dogs originated from outside the population; and that high levels of vaccination coverage may afford protection from rabies for up to 2 years.

Materials and methods

RESEARCH SITES

Data were collected from four communities, two in South Africa and two in Indonesia. The sites were selected during preliminary visits to Johannesburg and Bali in 2007 based on criteria including community support for the study, the absence of previous dog population management interventions by local animal welfare non-governmental organizations (NGOs) or authorities, geographical accessibility, operator safety and the availability of NGO support for data collection and translation. Rabies outbreaks occurred in Bali in 2008 and Gauteng Province in 2010.

The two sites in Gauteng Province, South Africa, comprised the informal settlement Zenzele west of Johannesburg (26·15°S and 27·41°E) and Braamfischerville in Soweto (26·12°S and 27·52°E). The study area encompassed the entire Zenzele township, whereas *c*. one-third of Braamfischerville was included in the study area to include a comparable number of dogs to Zenzele. In Indonesia, the two sites included the villages of Kelusa (8·26°S and 115·15°E) and Antiga (8·30°S and 115·29°E) on the island of Bali. In Kelusa, the study area encompassed the entire village with the exception of Banjar Yehtengeh, which is separated from the rest of the village by rice fields and jungle, the southern half of Banjar Peliatan and the entrances (i.e. a typical compound housing extended families) scattered along the main road leading into the village. In Antiga, the study area encompassed all of the main residential area (Banjars Kaler and Kelod). An additional area within Banjar Ketug included entrances scattered along a 2·7 km stretch of road winding through the jungle north of Kaler and Kelod.

All households in the study areas were included in the sampling frame. In Zenzele, the sample unit, or household, is a systematically numbered yard with usually one or two shacks and poor fencing. In Braamfischerville, a household is a systematically numbered yard with a small, fixed structure, and a variable number of shacks and variable quality fencing. In Bali, a household is equivalent to an 'entrance' associated with variable quality fencing. Given the lack of street names and house numbers, entrances were identified by photograph. With the exception of Zenzele, the study areas were established with no new households built during the study period. In May 2009, one new street of shacks was erected at the north end of Zenzele. Antiga and Zenzele are of comparatively lower socioeconomic status, and Banjar Ketug and Zenzele are without household sewage systems or water supply.

METHOD AND TYPE OF DATA COLLECTED

Individual-level data for every identified dog in the study area were collected longitudinally by direct observation and questionnaire from March 2008 until April 2011. The study population comprised of every owned dog (i.e. dog belonging to a household in the study area). Each owned dog was included in the study population immediately upon identification at its household and recorded by photograph (standardized dorsal and lateral views) and owner questionnaire and visually assessed (see below for more details). Pups were recorded but not photographed until their third month of life. Dogs were not photographed consistently during 2010 because handling that occurred due to rabies vaccination campaigns in that year (as part of the same research project) caused them to become flighty and difficult to photograph and because by that time the primary researcher and enumerators were familiar with the majority of dogs. Each dog in the study population was individually recognizable and monitored at its household through direct observation, by the primary researcher and enumerators, and questionnaire for the remainder of the study period or until it was lost from the study area.

Households were visited during door-to-door censuses undertaken every 3–4 months (3–5 months in Braamfischerville) during the study period. The first intercensus period was longer (Zenzele: *c*.5 months, Braamfischerville: *c*.8 months and Kelusa: *c*.4·5 months). Eleven censuses were undertaken in Zenzele and ten in Braamfischerville, ranging from 12 to 23 days and 16 to 31 days to complete, respectively. Nine censuses were undertaken in each of Kelusa and Antiga, ranging from 8 to 16 days and 11 to 19 days to complete, respectively. All households with female dogs were revisited by the enumerators between all the censuses. Therefore, every household in the study area was visited frequently during the study period, and most owned dogs were observed directly by the primary researcher and enumerators. However, a proportion of dogs were owned transiently between household visits and were not observed directly by the research team; these dogs were also recorded by owner questionnaire. These were generally young dogs that were acquired and then died between successive visits. Households were visited on foot during daylight hours and in approximately the same order.

In addition to owned dogs being monitored at their household, every dog encountered in a yard not their own or on the street during each census was identified by the primary researcher and enumerators as either belonging to a household in the study area or not. Each dog identified as not belonging to a household in the study area was classified as unowned. A description of the unowned dog was recorded, and, whenever possible, the dog was photographed. Only two dogs in Johannesburg and eighteen dogs in Bali were identified as unowned; these dogs were not included

in the study population but are reported separately (see *Ownership* in the Results).

Focus groups with community leaders, members and enumerators, including participatory rural appraisal (PRA) techniques (Kumar 2007), were undertaken in Zenzele during February 2008 to (i) investigate the ecology of the dog population in the study area and (ii) develop the questionnaires. See Appendix S1 (Supporting information) for a description of questionnaire development and implementation. Information collected, by direct observation and questionnaire, for every identified owned dog during each census and revisit included: house number, dog's name, age, gender, source, outcome (e.g. died, relocated), reason for ownership, physiological, clinical and (for females) reproductive status, nutrition (type and source), body condition score (BCS) and level of confinement. Body condition score was a surrogate for food volume given the practical limitations of quantifying food uptake from all possible sources, including owners. The dogs in Bali could not be readily handled. Therefore, a standard 9-point scoring system (emaciated score 1 to obese score 9) validated in adults (Laflamme 1997) and modified to assess body condition score without palpation was used. The modified system had been validated using dual energy x-ray absorptiometry in 71 dogs, including a small number of growing dogs (German & Holden 2006; German *et al.* 2006). Each dog, generally in its third month of life or older, received two independent body condition scores from the primary researcher and enumerators during each census or revisit. Clinical examinations were undertaken during each census by the primary researcher, a qualified veterinarian. The date and age of dogs at acquisition were reported by owners and/or visually assessed, including from the dentition of pups and juveniles (Dyce, Sack & Wensing 1987) in Johannesburg. For most dogs, these data were re-recorded at least once during the study period. The date a dog was lost from the study area was generally only recorded once. The month of loss was reported by the owner for 68% of the lost dogs in Zenzele, 78% in Braamfischerville, 51% in Kelusa and 55% in Antiga. Except where stated (see Table 4), the remainder were assumed to be lost uniformly between the census or revisit in which they were last recorded and the subsequent one. Apart from the primary researcher, all enumerators were local residents employed by NGOs. Data collection was standardized through detailed enumerator training at the start of the study and repeated on the first day of each census.

All known refuse in the study areas was evaluated non-systematically by the primary researcher. Refuse was photographed periodically, and its distribution and the presence of edible organic matter assessed subjectively at each visit.

Participatory approaches were preferred to mark–recapture or more technically demanding surveillance techniques, such as monitoring the movement of dogs with GPS collars, to further investigate the presence of a resident population of healthy, unowned dogs (i.e. dogs not belonging to households in the study area or outside the study area) in the Bali villages. Measurement error and statistical variation, violations of mark–recapture model assumptions and the need for repeat photographic mark–recapture preclude the use of these techniques to identify a real number of unowned, healthy dogs resident in the population, particularly where this subgroup is likely to be small. On this basis, participatory exercises were undertaken from April 2011 to April 2012 and are reported separately (Morters *et al.* in press).

ANALYTICAL METHODS

For the analysis, pups are defined as 0–3 months of age, juveniles 4–12 months of age and adults older than 12 months of age. Owned dogs were included in the analysis, once they reached their third month of life (i.e. *c.* 8 weeks of age) (hereafter referred to as 'registered' dogs). Pups born in households in the study area but lost before their third month of life, and unowned dogs are reported separately.

Nonparametric regression was used to explore trends in population size, mortality and pregnancy. Visual inspection of plots and autocorrelation and partial autocorrelation were used to assess periodicity, particularly seasonality, for these variables. An extended data set (i.e. by an additional 5 months) for Antiga was available.

The proportion of reproductively mature females pregnant per month was estimated to avoid variation in pregnancy confounded by any seasonal variation in population size, most likely from disease-induced mortality such as babesiosis which has a reported seasonal distribution (Collett 2000). Bitches continually confined to a dog proof yard were excluded from these analyses. Monte Carlo estimates of the proportion of females in early (i.e. not visible) pregnancy when lost from the study populations were obtained by sampling from the observed distributions of age at first pregnancy and interval between the first and subsequent litters. Mortality was also estimated as the proportion of dogs dying per month and in terms of total mortality, specific disease-induced mortality and 'other' (i.e. disease-induced mortality and dogs found dead, missing entries and unknown causes).

We used Cox proportional hazard models to evaluate the risk of loss from the starting cohorts by age class at the start of the study and by gender. To model declines in vaccination coverage, estimates of vaccination coverage were obtained by assigning a random sample of dogs from the starting cohort equal in size to the proportion assumed to be vaccinated and determining those still present at 12 and 24 months. This process was repeated 1000 times to produce Monte Carlo estimates of vaccination drop-off. A Bayesian ordinal regression framework (McKinley, Morters & Wood, in press) was used to investigate whether there were clear trends between body condition and increased caloric requirements from growth and lactation (National Research Council 2006). All observations with complete information for the variables of interest (Table S23, Supporting information) were included in the analyses. To account for observer variability, we fitted four versions of the model using minimum or maximum BCS (between observers) as response variables and two definitions of gestation and lactation [estimated (63 days gestation and 12 weeks lactation) and observed]. Analysis was repeated without the first time point (i.e. censuses March–May 2008) to allow for owner-reported clinical signs for the previous 3 months. We tested for an association between population size and births and deaths.

Data analyses were conducted using R (R Core Team 2013) and C.

The study was approved by the Cambridge University Department of Veterinary Medicine Ethics Committee. Research permits were granted by the Ministry for Research and Technology (RISTEK), Indonesia. Equivalent permits to collect demographic data were not required in South Africa. In all sites, informed verbal consent was obtained prior to each survey from the

community leaders and respondents, who were kept fully informed of the purpose, approach and progress of the study.

Results

STUDY POPULATION

Throughout the study, there was a very high level of compliance, with a low rate of partial and non-respondents (Zenzele 1·5%, Braamfischerville 1·2%, Kelusa 2·5% and Antiga 2·2%). While some respondents declined to complete the full questionnaire, all provided partial information, such as the number, source and outcome, and permitted visual assessment of their dogs periodically throughout the study period. A total of 3240 owned dogs were registered during the study period: 1022 in Zenzele, 882 in Braamfischerville, 707 in Kelusa and 629 in Antiga (Table S1, Supporting information). Unless stated otherwise, all results pertain to these dogs.

The sex ratio was approximately even in Johannesburg but skewed (male:female 75:25) in Bali through killing of unwanted female puppies (Tables S2–S3, Supporting information), and most dogs were adult (Fig. S1, Supporting information). The majority (>90%) of dogs were free to roam intermittently or continuously in Zenzele, Kelusa and Antiga, whereas in Braamfischerville, *c*. 40% of dogs were confined most of the time (Table S4, Supporting information). Most dogs were not sterilized except for 14·1% and 26·9% of male dogs in Kelusa and Antiga, respectively. These dogs were 'traditionally' castrated by a community member at about 6 months of age (Table S5, Supporting information).

POPULATION SIZE

Variations in population sizes are shown in Fig. 1 and Table S6 (Supporting information) (and age class at registration Table S7, Supporting information). Overall, there was a decline in population size in Zenzele (linear regression $P < 0{\cdot}001$) and Antiga ($P < 0{\cdot}001$), while the population remained constant in Braamfischerville ($P = 0{\cdot}6$) and Kelusa ($P = 0{\cdot}5$), with no seasonal variation evident. The population decline in Antiga from March 2010 may be attributed to fewer dogs being gained during this period than prior to March 2010 (Mann–Whitney U-test $P = 0{\cdot}01$), whereas a similar number of dogs were lost during both periods ($P = 0{\cdot}5$) (the mean number of dogs gained per month before March 2010 was 12·4 and from March 2010 was 7·3; the mean number of dogs lost before March 2010 was 10·6 and from March 2010 was 12·5). Population size (and density) varied overall by a maximum of 22·1% (ranging from 3·8%) from the mean. The mean number of dogs gained and lost per month ranged between 10·3–18·7 and 11·4–20·3, respectively (Tables S8–S9, Supporting information). With the exception of Antiga, the percentage of dog-owning households was constant (Zenzele 10·0% at the start of the study and 12·0%

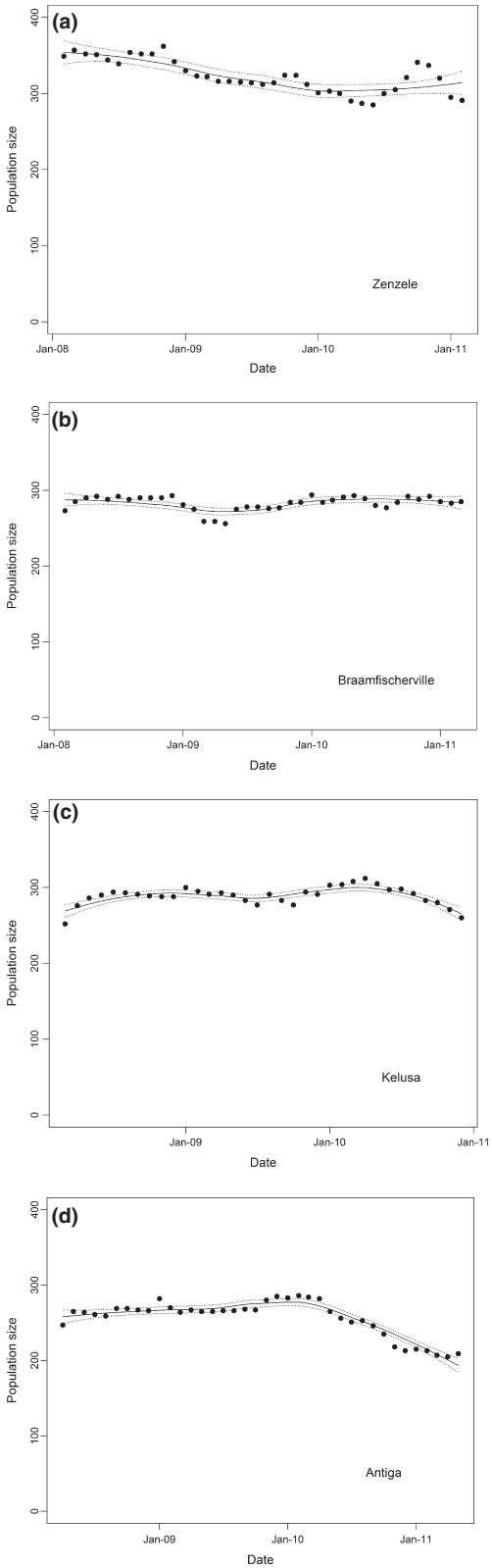

Fig. 1. Variations in population size for the study period: (a) Zenzele, (b) Braamfischerville, (c) Kelusa, and (d) Antiga. Each large dot represents the number of dogs in the registered population at the end of that month after accounting for the dogs gained and lost during that month. The nonparametric regression line (-) shows the average variation in population size during the study period, and the dotted lines (.) the 95% confidence intervals for the mean.

at the end, Braamfischerville 7·5% and 7·8%, Kelusa 71·9% and 72·9%, and Antiga 49·0% declining to 41·6%), and the number of dogs per dog-owning household was unchanged at *c.* 1·3 in Johannesburg and Antiga and 1·7 in Kelusa (Table S1, Supporting information).

In Zenzele, Braamfischerville, Kelusa and Antiga, 7·9%, 26·1%, 2·0% and 4·5% of the registered dogs, respectively, were reported as present during the previous inter-census or revisit period by respondents but were not observed directly by the primary researcher and enumerators. Excluding the non-observed dogs from the data set for Zenzele, Kelusa and Antiga did not change the trends in population size. However, removal of non-observed dogs from Braamfischerville resulted in an overall increase in population size during 2008 and 2009 when the interval between surveys was intermittently longer than the other sites.

DEMOGRAPHIC PROCESSES

There was no overall increase or decrease in the proportion of dogs pregnant and dying per month, and there was no seasonal variation (Tables S10–S14, Supporting information). In Kelusa, total and 'other' mortality for the entire study population increased significantly with time ($P < 0{\cdot}001$), and there was an overall increase in juvenile mortality ($P < 0{\cdot}01$). In Zenzele, juvenile mortality during the first intercensus period was lower than during the rest of the study period. Exclusion of this period (or even the first 2 months of the study) resulted in constant juvenile mortality ($P = 0{\cdot}2$).

At least one-third of the population was sourced from outside the study area (Zenzele 40·8%, Braamfischerville 59·5%, Kelusa 36·5%, Antiga 43·0%) (Table 1). Owners reported a variety of reasons for obtaining a dog from outside the research site (see Materials and Methods) although the most common reason was opportunism (Tables S15–S16, Supporting information). Most owners had planned to get a dog (Table S17, Supporting information), including a proportion (Zenzele 56%, Braamfischerville 74%, Kelusa 16% and Antiga 11% minimum) of those who found their dog by chance outside the research site. There was no overall increase or decrease in the proportion of dogs acquired from outside the study area per month (Table S18, Supporting information). Less than one-third of the dogs were born in the household, and 50% or less were born in the study area (Zenzele 50·2%, Braamfischerville 16·0%, Kelusa 37·8% and Antiga 31·3%). A substantial proportion (15–20%) of dogs disappeared, were stolen or unaccounted for (Table 2). Table S19 (Supporting information) shows the outcomes of pups born in study households.

DECLINES IN THE STARTING COHORTS

At least 20% (Zenzele 28·2%, Braamfischerville 23·9%, Kelusa 39·6% and Antiga 51·7%) of the dogs registered during the starting censuses were present 3 years later at the end of the study (Fig. 2). Assuming 60% vaccination coverage of the starting cohort, coverage was estimated to decline to between 22 and 33% after 24 months, and assuming an initial coverage of 80%, coverage would be expected to decline to between 29 and 43% after 24 months (Table 3). The yearly relative decrease in the starting cohorts varied across age classes, with greatest declines recorded in younger age classes (Table 4). In Bali, dogs that were adults at the start of the study remained in the starting cohorts on average significantly longer than those that were juveniles and pups ($P < 0{\cdot}001$). Similar trends were observed in Johannesburg (S20–S21). Table S22 (Supporting information) shows the outcomes of the dogs in the starting cohorts.

Table 1. Sources of the registered dogs

	Zenzele (%)	Braamfischerville (%)	Kelusa (%)	Antiga (%)
Sourced as pups				
Born at address	128 (19·0)	60 (9·9)	128 (28·1)	87 (24·5)
Elsewhere in study area	210 (31·2)	37 (6·1)	44 (9·7)	24 (6·8)
(address not reported)	(98)	(4)	(20)	(6)
Non-study area of the research site	NA	12 (2·0)	12 (2·6)	10 (2·8)
Research site but area not known	NA	78 (12·8)	73 (16·0)	47 (13·2)
Outside research site	186 (27·6)	221 (36·3)	120 (26·4)	112 (31·5)
Not known	25 (3·7)	25 (4·1)	28 (6·2)	20 (5·6)
Sourced as juveniles or adults*				
Non-study area of the research site	NA	5 (0·8)	0	3 (0·8)
Inside study area	11 (1·6)	0	0	0
Research site but area not known	NA	21 (3·4)	10 (2·2)	7 (2·0)
Outside research site	89 (13·2)	124 (20·4)	34 (7·5)	28 (7·9)
Not known	24 (3·6)	26 (4·3)	6 (1·3)	17 (4·8)
Total acquired	673	609	455	355

*Includes a small number of dogs where the age at acquisition was not reported but was most likely juvenile or adult.

Table 2. Outcomes of the registered dogs

	Zenzele (%)	Braamfischerville (%)	Kelusa (%)	Antiga (%)
Died	513 (70·2)	355 (59·5)	322 (72·0)	264 (68·4)
Disappeared	58 (7·9)	30 (5·0)	58 (13·0)	39 (10·1)
Stolen	23 (3·1)	38 (6·4)	0	0
Given away in the non-study area of the research site	NA	13 (2·1)	3 (0·7)	4 (1·0)
Given away outside research site	40 (5·5)	66 (11·1)	14 (3·1)	26 (6·7)
Given to meat trader	NA	NA	18 (4·0)	14 (3·6)
Relocated outside research site with owner	39 (5·3)	34 (5·7)	11 (2·5)	7 (1·8)
Dumped	0	0	0	5 (1·3)
Other	1 (0·1)	0	0	2 (0·5)
Unaccounted for	44 (6·0)	47 (7·9)	17 (3·8)	19 (4·9)
Given away in study area but not found by enumerators	13 (1·8)	2 (0·3)	0	0
Given away in research site but area not known	NA	12 (2·0)	4 (0·9)	6 (1·6)
Total lost	731	597	447	386

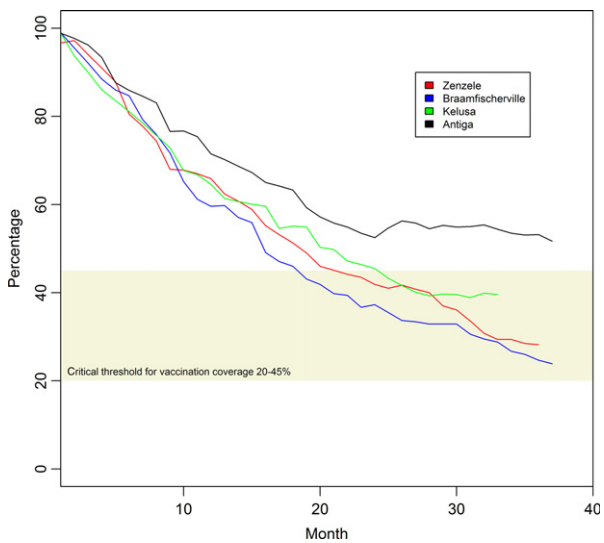

Fig. 2. Declines in the starting cohorts for the study period, generated by plotting the number of dogs remaining from each starting cohort that month as a percentage of population size that month. The beige region indicates the vaccination coverage (of 20–45%) required to interrupt rabies transmission in a population (Hampson *et al.* 2009).

Table 3. Mean estimates of vaccination coverage with time (95% confidence intervals)

	% of the population vaccinated at month 0	% vaccination coverage after month 12	% vaccination coverage after month 24
Zenzele	60	40·0 (40·0–40·1)	26·1 (26·0–26·1)
	80	53·4 (53·4–53·5)	34·9 (34·9–35·0)
Braamfischerville	60	37·0 (36·9–37·1)	22·0 (21·9–22·1)
	80	49·3 (49·2–49·3)	29·2 (29·1–29·2)
Kelusa	60	40·2 (40·1–40·3)	27·4 (27·3–27·4)
	80	55·8 (55·8–55·9)	36·6 (36·5–36·7)
Antiga	60	43·2 (43·1–43·3)	32·6 (32·5–32·7)
	80	57·5 (57·4–57·6)	43·3 (43·2–43·4)

OWNERSHIP

The participants of the Zenzele focus group agreed unanimously that all of the dogs residing in the study area were owned. Similarly, almost all of the dogs in Johannesburg identified by the primary researcher and enumerators were owned by households in the study areas. One healthy dog in Zenzele and one in Braamfischerville did not belong to a household in the study area (0·1% of all observed dogs in their third month of life or older in each study area); these dogs were each observed on only one occasion. One other dog owned by a household in Zenzele was abandoned. The dog was subsequently observed during successive survey periods around the rubbish heaps on the outskirts of the study area in worsening body condition (BCS 1–2); until, it was eventually adopted by a neighbouring household.

Almost all of the dogs identified in the Bali sites were also owned by households in the study areas. Eight dogs in Kelusa and ten in Antiga did not belong to households in the study areas (1·1% and 1·5% of all observed dogs in their third month of life or older in each study area, respectively). All of these dogs were observed on only one occasion, and almost all (12/16) were emaciated (BCS ≤2) and had severe generalized dermatitis (16/18). Although residents in the vicinity reported that at least six of these dogs were unowned, it was not verified if these dogs were owned by households outside the study area or were indeed unowned. In Kelusa and Antiga, 3·1% and 5·3%, respectively, of dogs owned by households in the study areas had BCS ≤2 and suffered from generalized dermatitis either consistently or transiently during the study period.

Table 4. Declines in number of dogs in the starting cohorts by age class and gender (males: females). The numbers of dogs are based on individual-level mid-point data which is a close approximation to the population-level averaged data

	Initial cohort of dogs	Declines in cohort 0–12 months	Declines in cohort 0–24 months	Declines in cohort 0–36 months
Zenzele				
Adults	276 (147:128)*	41·3% (65:48)	61·6% (90:79)	75·4% (109:98)
Juveniles	73 (37:36)	43·8% (19:13)	76·7% (28:28)	84·9% (31:31)
Pups	20 (14:6)	65·0% (7:6)	75·0% (8:7)	85·0% (10:7)
Braamfischerville				
Adults	221 (113:107)*	41·6% (43:48)	60·6% (63:70)	72·9% (75:85)
Juveniles	52 (33:19)	65·4% (22:12)	82·7% (27:16)	88·5% (30:16)
Pups	15 (6:9)	53·3% (4:4)	66·7% (5:5)	86·7% (6:7)
Kelusa				
Adults	209 (158:51)	27·3% (38:19)	44·5% (62:31)	58·4% (82:40)†
Juveniles	43 (33:10)	55·8% (17:7)	60·5% (19:7)	72·1% (23:8)†
Pups	27 (17:9)*	51·9% (10:3)	74·1% (13:6)	85·2% (13:9)†
Antiga				
Adults	217 (172:43)‡	24·4% (38:14)	38·2% (59:23)	53·9% (86:30)§
Juveniles	32 (20:12)	43·8% (8:6)	68·8% (14:8)	81·3% (17:9)§
Pups	19 (12:7)	52·6% (7:3)	73·7% (10:4)	89·5% (12:5)§

*The gender was not reported for one dog.
†0–33 months.
‡The gender was not reported for two dogs.
§0–37 months.

The majority of respondents in Bali (Kelusa 84% and 90% and Antiga 85% and 88% during the April 2008 and January 2009 censuses, respectively) reported that there were no unowned dogs in either their banjar (April 2008) or village (January 2009). Most remaining respondents (71%) reported ≤10 unowned dogs in the banjar and village. These respondents assumed that dogs were unowned on the basis that they roamed (38%) and were often in poor condition or 'uncared for' (48%) rather than known ownership status. Although limited to dog-owning respondents, given that most households have experience of owning a dog, these data may reflect community opinion overall.

FOOD SOURCES

Almost all owned dogs had been reportedly fed by their owner on the day of the interview or the previous day. In Zenzele, Braamfischerville, Kelusa and Antiga, 2·6%, 0·6%, 0·1% and 1·1%, respectively, of dogs were last fed at least 2 days prior to the interview on one occasion and in Antiga, 0·7% on more than one occasion. Only one juvenile in Antiga was reported as 'never fed' by the owner; however, long-term feeding patterns for this dog could not be established because it died 2 months after registration.

Most of the rubbish in the study areas consisted of inedible, inorganic matter. The remainder was poor-quality organic matter, including food waste. Rubbish heaps around the periphery of Zenzele were removed by the community during the winters of 2009 and again 2010 after re-accumulation. The local authorities regularly collected household waste in Braamfischerville and very occasionally in Zenzele. In Kelusa and Antiga, organic matter was often incinerated or fed to pigs and occasionally used as compost. None of the sites were within 5 km of alternative food sources such as municipal rubbish dumps or commercial abattoirs.

Body condition scores were generally unimodal including individuals expected to have increased energy requirements from growth and lactation (Fig. S2, Supporting information). Although, on average, lactating individuals were thinner than non-lactating females and males, most were not underweight and body condition ranges were similar to non-lactating females and males. Overall, there was no tendency for growing individuals (i.e. pups and juveniles) to be thinner than adults (Tables S23–S27, Supporting information). Rather, on average, young adults (13–36 months) had less subcutaneous fat than the other age classes probably consistent with normal anatomical variation (Lund *et al.* 2006). There was no interaction between age and lactation on body condition. Furthermore, even though sterilized dogs were on average fatter than unsterilized dogs, the relationship between body condition and age was similar for all four sites including Johannesburg where most dogs were not sterilized. There was no association between body condition and the number of dogs in the household.

Discussion

The longitudinal, individual-level data in this study provide the most detailed demographic data currently available for domestic dogs in low-income communities in Asia and Africa and provide valuable support for

planning disease and population control programmes and parameterization of epidemiological models of infectious diseases, including rabies, in these settings.

A key finding was that almost all of the identified dogs were owned by households in the study area, despite the vast majority being free-roaming, and were accessible for evaluation and vaccination. Our results are consistent with an interpretation that dog population size in these communities is regulated by human demand for dogs, not environmental resource constraints (i.e. food from refuse). We observed a range of body condition scores for these dogs regardless of energy requirements dependent on age or reproductive status, including lactation when energy requirements can be more than double (National Research Council 2006). This is consistent with owners reporting that most dogs were fed individually at the household on a regular basis. The low nutritional value of the refuse, and extremely poor body condition of most dogs not owned by households in the study area, also suggests that environmental resources were probably inadequate to meet the energy requirements of those dogs not fed properly by an owner and that these dogs would not be able to survive in these environments without provisioning. Consistent with studies of environmental resource constraints in feral ungulate and wildlife populations (Clutton-Brock, Major & Guinness 1985; Coulson *et al.* 2001; Bonenfant *et al.* 2002), where mammalian population sizes fluctuate around K (Sibly & Hone 2002), if dogs are competing for environmental resources at the population level, then thin individuals may be those with the highest energy requirements. Although this association could be obscured by behaviours, such as hunting, domestic dogs are predominately scavengers (Bradshaw 2006) and, where refuse is the main environmental resource available to scavenge, such as in this study, this is unlikely. Thus, our data suggest that free-roaming, domestic dogs are not 'wildlife', competing for environmental resources to survive; rather, humans are responsible for providing adequate care for this domesticated species. Furthermore, while our observations were intermittent and limited to daylight hours, we did not observe a resident population of dogs in reasonable or good body condition that were not fed daily by an owner. Overall, these observations were consistent with community opinion expressed during this current study, and participatory exercises undertaken in Kelusa and Antiga during 2011 and 2012 that utilized systematic ranking methods to obtain consensuses regarding the food sources of free-roaming dogs (Morters *et al.* in press). While our findings may not be universally applicable, they agree with previous studies, primarily in sub-Saharan Africa, that report the majority of free-roaming dogs as owned and fed regularly by their owners (Brooks 1990; de Balogh, Wandeler & Meslin 1993; Butler & Bingham 2000).

Data from this study demonstrate the contribution of different demographic processes, including human-mediated movement, to variations in population size and support the view that dog population size is primarily a function of human factors. However, the cultural, economic and social factors driving the rates of acquisition and disposal of dogs (and thus ownership) are still poorly understood and warrant further investigation. This includes responses by community members to fear of rabies or liability arising from dog bites to people in rabies-endemic areas. Indeed, a reluctance to acquire dogs because of rabies may have driven the declines in the Bali populations from January 2010 in the wake of a rabies epidemic. Population growth may, in part, be limited in established communities where geographical expansion is minimal and the number of household units relatively stable, such as in this study. Previous estimates of growth have generally been at the national (Brooks 1990) or district (Butler & Bingham 2000; Kitala *et al.* 2001; Hampson *et al.* 2009) level and may be reliable when considering the ecological heterogeneity within, and limited movement of dogs into and out of, large geographical areas. However, human-mediated movement of dogs, including over large geographical distances, can seed incursions of rabies and make endemic transmission more difficult to interrupt (Denduangboripant *et al.* 2005; Talbi *et al.* 2010; Townsend *et al.* 2013). Therefore, the level or scale of interventions for control programmes and policy needs to be considered carefully.

This study also has important implications for the design of vaccination campaigns, as the frequency of campaigns required to maintain vaccination coverage above the critical threshold of 20–45% (Hampson *et al.* 2009) depends on the introductions of susceptible individuals into the population by people through the acquisition of dogs born locally or from outside the population and the loss of vaccinated individuals through deaths and the relocation of dogs by people. We observed variable declines in the starting cohorts with time and age class. If 100% of these dogs had been vaccinated against rabies, and given the rates of birth, death and human-mediated movement recorded in this population, coverage sufficient to disrupt rabies transmission would have been maintained throughout the 3-year study period when using vaccine with a 3-year duration of immunity. More realistically, vaccination coverage tended to fall in the range of 60–80%, with 80% achieved in the study areas during 2010, including the Bali sites where the dogs were less easy to handle. In these situations, vaccination coverage following a single campaign would decline to threshold levels after 2 years. Similar levels of vaccination coverage have been readily achieved in Africa (Kaare *et al.* 2009) and Asia (Bogel & Joshi 1990), and these results emphasize that the benefits of vaccination campaigns can be long-lived.

Our findings have practical consequences in terms of dog population control. Mass sterilization programmes, often used as an adjunct to vaccination and advocated as a necessary component of dog rabies control, will have a limited effect where population growth is limited, and a large proportion of the population originates from outside

the area. Furthermore, given the ongoing demand for dogs, any reduction in the local supply of puppies from sterilization, or following a cull, might result in further movement of dogs by people into communities from outside, compounding the risk of disease introduction.

Our results demonstrate the importance of human factors in the design and implementation of disease and population control programmes and epidemiological models. Although owners generally facilitate vaccination of their dogs against rabies, movement of dogs by people can increase the spread of rabies necessitating widespread and sustained vaccination programmes in rabies-endemic areas. Human factors are therefore critical factors that must be considered in the development of disease and population control programmes.

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Supporting Information

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

Appendix S1. Questionnaire development and implementation.

Appendix S2. Sex ratios (also see Tables S2 and S3).

Appendix S3. Population age structure (and see Fig. S1).

Appendix S4. Confinement (also see Table S4).

Appendix S5. Reproductively capable bitches (also see Tables S10 and S11).

Appendix S6. Mortality of registered dogs (also see Tables S12–S14).

Appendix S7. Reasons for sourcing of dogs outside of the research sites (also see Tables S15–S17).

Appendix S8. Outcome of pups (also see Table S19).

Appendix S9. Unknown sources and outcomes of dogs (also see Tables 1 and 2 and S19).

Table S1. Household characteristics.

Table S2. Sex ratios.

Table S3. Litter sizes.

Table S4. Confinement status.

Table S5. Sterilization status.

Table S6. Population size and density.

Table S7. Age class at registration.

Table S8. Number of dogs gained into the registered population.

Table S9. Number of dogs lost from the registered population.

Table S10. Pregnancy rates.

Table S11. Litters per month.

Table S12. Total mortality.

Table S13. Juvenile mortality.

Table S14. Causes of mortality.

Table S15. Reasons for sourcing a dog from outside the Johannesburg sites.

Table S16. Reasons for sourcing a dog from outside the Bali sites.

Table S17. Approach to dog acquisition by owners.

Table S18. Rate of acquisition from outside the study areas.

Table S19. Outcomes of pups.

Table S20. Average time to loss or censoring of the starting cohorts.

Table S21. Risk of loss from the starting cohorts by age class and gender.

Table S22. Outcomes of dogs in the starting cohorts.

Table S23. Variables included in the ordinal regression models.

Table S24. Ordinal regression model results for Zenzele.

Table S25. Ordinal regression model results for Braamfischerville.

Table S26. Ordinal regression model results for Kelusa.

Table S27. Ordinal regression model results for Antiga.

Fig. S1. Age structures for the registered population.

Fig. S2. Distributions of the ordinal regression model explanatory variables.

