Deriving dispersal distances from genetic data

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Dispersal is one of the most important factors determining the genetic structure of a population, but good data on dispersal distances are rare because it is difficult to observe a large sample of dispersal events. However, genetic data contain unbiased information about the average dispersal distances in species with a strong sex bias in their dispersal rates. By plotting the genetic similarity between members of the philopatric sex against some measure of the distance between them, the resulting regression line can be used for estimating how far dispersing individuals of the opposite sex have moved before settling. Dispersers showing low genetic similarity to members of the opposite sex will on average have originated from further away. Applying this method to a microsatellite dataset from lions (*Panthera leo*) shows that their average dispersal distance is 1.3 home ranges with a 95% confidence interval of 0.4–3.0 home ranges. These results are consistent with direct observations of dispersal from our study population and others. In this case, direct observations of dispersal distance were not detectably biased by a failure to detect long-range dispersal, which is thought to be a common problem in the estimation of dispersal distance.

Keywords: dispersal; dispersal distance; gene flow; lions; *Panthera leo*

1. INTRODUCTION

Estimating dispersal distances and rates in the wild is often difficult and has previously relied mainly on capture–mark–recapture techniques. In most studies the fates of many dispersing individuals are simply not known (Koenig *et al.* 1996) due to the logistical problem of monitoring individuals that leave a study site. In addition, some immigrants in most studies are of unknown origin (Koenig *et al.* 1996; Dieckmann *et al.* 1999).

However, patterns of dispersal are of major importance to the genetic structuring of a population (Chesser *et al.* 1993; Dobson *et al.* 1997) and dispersal versus philopatry plays a crucial role in the evolution and maintenance of sociality (Emlen 1982; Waser 1996; Perrin & Mazalov 1999). From an ecological viewpoint, dispersal can affect a species' abundance and distribution (Dieckmann *et al.* 1999). Despite its fundamental importance, data on dispersal distances are surprisingly limited, even for species that have been extensively studied (Waser 1996).

In species where one sex shows strong philopatry and the other disperses, genetic data contain information about dispersal distances. In this paper, we illustrate this principle by deriving dispersal distances for male lions from microsatellite data. Lion prides occupy a permanent territory and display a number of cooperative behaviours, such as cooperative hunting (Schaller 1972) and territorial defence (McComb *et al.* 1994). Female offspring are usually recruited into the pride, whereas male offspring invariably disperse when reaching adulthood (Pusey & Packer 1987). Approximately one-third of females leave their natal pride and establish a new pride. Such settlements are always located adjacent to their natal range, often including part of their old range. Female dispersal is thus extremely limited in space. Dispersing females breed at a later age and have higher mortality than non-dispersers

(Pusey & Packer 1987), further reducing the genetic effects of female dispersal on gene flow.

Because their dispersal is highly sex biased, lions are well suited for our procedure. First, pairwise estimates of relatedness (r) are needed for the philopatric sex (which is females in lions). Second, these pairwise comparisons are plotted against a measure of geographical distance between the pair members. A regression line fitted to this plot will show how genetic relatedness drops off with distance for the philopatric sex in the population. Lastly, by calculating the pairwise relatedness estimates between pride-holding males and their females one can use the regression for inferring the distance moved by males before joining a pride. Essentially, genetic similarity among members of the philopatric sex provides a standard against which dispersing individuals can be compared (just as one could pick two females, determine their relatedness and estimate their spatial separation in the population).

2. METHODS

(a) *Study site and fieldwork*

All data were collected from a free-ranging lion population in the northern sector of the Selous Game Reserve in southeastern Tanzania (73°5' S, 38°15' E) from June 1993 to February 1999. The study site covered *ca.* 1000 km² and consisted mostly of wooded savannah, thorn woodland, miombo and *Combretum* thickets.

We mainly identified individual lions from their whisker spot patterns (Pennycuik & Rudnai 1970) aided by the use of a picture library, but other external attributes were also used. A total of 141 lions in 16 prides were identified during the study. Anaesthesia was induced in females fitted with radiocollars (MOD-500 Telonics, Mesa, AZ, USA) using 200 mg Telazol (Tiletamine-zolazepam) and 100 mg Rompun (Xylazine). We administered drugs by dart from 10–15 m away, darting from inside a vehicle with a Telinject (Saugus, CA, USA) (Vario 3V) CO₂ rifle. We reversed the effects of Xylazine by injecting 17 mg

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of Yohimbine intravenously within 45 min of the initial darting, when the lion showed some signs of recovery. Lions were usually mobile without visible signs of anaesthesia 2 h after the injection of Yohimbine.

We collected tissue biopsies using a CapChur CO₂ pistol, with biopsy darts developed from plans by Karesh *et al.* (1987). The lions typically reacted to the impact of the dart by startling, often growling and moving away a few metres, but usually resettling, which allowed sampling of several animals per session. The tissue biopsies were stored in 100 mM EDTA 95% ethanol solution at ambient temperatures in the field and at -20°C in the laboratory.

(b) *Molecular methods*

DNA was extracted using a standard phenol/chloroform protocol (Maniatis *et al.* 1982), dissolved in water and stored at -20°C . Fluorescently labelled primers (the dyes HEX, TET and FAM) were run in 10 μl triplex reactions. The polymerase chain reactions (PCRs) included 25 ng target DNA, 2.5 nmol dNTP, 4 pmol of each primer, 0.4 units of Taq polymerase and 1 PE buffer (including 15 mM MgCl₂) and were typically run at 94°C for 3 min, with 25 cycles at 94°C for 30 s, 52°C for 45 s and 72°C for 1 min, followed by 72°C for 10 min. Two microlitres of PCR product was mixed with 6 μl formamide and 0.03 μl GS500 TAMRA size standard and run on an ABI Prism 310 Genetic Analyzer (PE Applied Biosystems, Foster City, CA, USA). The triplex combinations were Fca001–Fca031–Fca506, Fca008–Fca026–Fca045, Fca077–Fca126–Fca149, Fca272–Fca567–Fca628 and Fca275–F115–Fca391. Fca149 was subsequently dropped from the analyses due to ambiguous results, leaving a total of 14 loci with an average heterozygosity level of 0.75 ± 0.08 (mean $\pm$ s.d.).

(c) *Data analysis*

All of our genetic data are derived from 47 individuals. The regression of genetic distance to spatial distance is based on data from 33 females in 14 prides. The data on the genetic similarity of males to females come from 14 males in 6 male coalitions holding tenure in 7 of the 14 prides (one coalition held two prides simultaneously). During our 5.5 years of observation, only two adult females (out of ca. 60 adults) were observed to disperse out of their pride of birth, similar to patterns reported for other populations (Pusey & Packer 1987). We calculated male-to-female genetic similarity across all possible dyads. Estimates of relatedness (r) were obtained using the software RELATEDNESS (Goodnight & Queller 1999) and F -statistics were obtained with the software ARLEQUIN (Schneider *et al.* 2000).

We expressed distance as the number of home ranges apart (so that zero represents pride mates) for the regression of relatedness on the distance between pairs of females. Because pride and territory sizes vary, this method measures distance in a way that has clearer biological meaning than simple linear distance. The data points for this regression have an unusual sampling structure because each point comes from a pair of individuals. Each lioness contributes to more than one data point, but the data do not follow a nested design, so parametric estimates of confidence intervals suitable for repeated measures (e.g. from PROC MIXED) were not possible. Consequently, we generated confidence intervals for the regression from 5000 bootstrap samples of genetic similarity for each distance. Statistical analyses were performed in STATISTICA and Microsoft EXCEL, using the add-in POPTOOLS for bootstrap resampling (which can be downloaded from <http://www.dwe.csiro.au/vbc/poptools/>).

3. RESULTS

As expected, the genetic similarity among females (Queller–Goodnight r) was significantly correlated with spatial distance (Mantel test, $n=528$ and $p < 0.001$) (figure 1).

The mean relatedness among female pride mates, as estimated by the regression line, is just below 0.2, similar to the directly measured unbiased mean (0.26).

(a) *Mean dispersal distance*

The mean genetic similarity between males and females can be used to infer the male dispersal distance using the relationship between genetic similarity and distance described for females (figure 1). The majority of males showed low genetic relatedness to the females in their pride (mean Queller–Goodnight $r = -0.023$) (see also Packer *et al.* 1991), although one pride had closely related males holding tenure. Following the logic outlined in § 1, our measure of genetic similarity for Selous lions suggests a mean dispersal distance of 1.3 prides.

(b) *Minimum and maximum dispersal distances*

We derived the minimum and maximum dispersal distances for males from the 95% confidence intervals of the regression of genetic similarity (among females) on spatial distance and the 95% confidence interval of the estimated mean genetic similarity between males and females (figure 1). First, we regressed genetic similarity among females on distance. Then, we used the mean genetic similarity of males to females for identifying the mean dispersal distance from the regression line and by horizontal extrapolation from this intercept we derived the 95% confidence limits of the mean dispersal distance (dashed lines in figure 1), resulting in a range of 0.8–1.8 home ranges dispersed. Finally, we combined the confidence limits of the mean genetic similarity and the confidence limits of the regression in order to extract the overall 95% confidence limits of the mean dispersal distance (stippled lines in figure 1), resulting in a range of 0.4–3.0 home ranges.

4. DISCUSSION

As predicted by theory, our estimate of genetic similarity among females shows a decline with distance. Genetic similarity should asymptote for estimates of r once a pair of individuals is sufficiently distant from one another. This is expected because, for any pattern of dispersal, there should be a distance beyond which identity by descent will be very uncommon. However, the regression line in figure 1 actually shows an increase in the right part of the graph. We believe this is due to random error since the data are limited to two prides (and only six individuals) for the pairwise comparisons of individuals seven prides apart.

Using F_{ST} as the genetic distance measure rather than relatedness conceptually presents no problems. However, using F_{ST} for our small dataset gave confidence intervals so wide that nothing could be inferred about the dispersal distance. However, because F_{ST} is not expected to asymptote as distance increases (unlike r), it may provide better information for species where dispersers move a large

Figure 1. Estimates of r for pairs of females plotted against the number of pride ranges apart (0 = within prides, 1 = neighbouring prides, etc.). The dashed curves show the 95% confidence bands. The vertical dashed lines identify extrapolated 95% confidence intervals for the mean dispersal distance estimate (0.8–1.8) due to the uncertainty of the regression line. The vertical stippled lines identify extrapolated the overall 95% confidence intervals for the mean dispersal distance (0.4–3.0). The fitted lines are least-square regressions based on the means and confidence intervals derived by bootstrapping (see §2).

number of home ranges, particularly for the upper limit on dispersal distance. Until the method has been applied to more datasets, it is difficult to predict whether F_{ST} or r (or both) will provide the best resolution of dispersal distances.

Female lions are not perfectly philopatric. Approximately 20% of females emigrate, invariably settling adjacent to their natal territory. Somewhat surprisingly, we suggest that this movement by females does not produce a systematic bias in estimates of the dispersal distance for males (figure 2). In some cases, a male may move in the same direction as a previous, recent movement by females and genetic data will underestimate his dispersal distance (figure 2a). On the other hand, a male may move in the opposite direction and genetic data will overestimate his movement (figure 2b). If dispersal is not in a consistent direction, then these errors will cancel out and genetic data will give an unbiased estimate of the mean dispersal distance. That said, prior movements (by either sex) will inflate the variance in genetic estimates of dispersal distance. It is difficult to envision circumstances in species with a continuous distribution in which non-random dispersal will have a major influence on the dispersal distance estimated by our method. However, patterns of dispersal could be highly biased in some circumstances, for example in species that have a patchy distribution, at the edge of a population's distribution or in cases where dispersal follows habitat corridors.

Another caveat is that dispersers will not have an impact on the gene pool unless they breed. It is conceivable that individuals that have dispersed further have different reproductive success to those that have dispersed shorter distances. Therefore, caution should be used before applying derived distances to genetic models. A previous study of dispersal in lions showed that many dispersal events were of short distance (as in our study), but also found that 69% of males entered the study area

Figure 2. Patterns of movement by the 'philopatric' sex affecting dispersal estimates. (a) Genetic data will underestimate the dispersal distance since close relatives are found in a neighbouring pride, despite the actual dispersal distance being two prides away. (b) The opposite holds true: genetic data will overestimate the dispersal distance since close relatives can be found two prides away even though dispersal only occurred over one pride range.

from elsewhere (Packer & Pusey 1993). This precluded an estimate of the average dispersal distance because distance was simply unknown for most males. The genetic data from the Selous Game Reserve suggest that

many of these unknown immigrants probably originated from just outside the study area if the patterns of dispersal are similar in the two populations. This comparison illustrates the practical utility of the new method. Tracking dispersing individuals quickly becomes logistically very demanding and determining the origin of immigrants is often impossible, even in well-designed, long-term studies such as the Serengeti lion study (Packer & Pusey 1993). Finally, this comparison suggests that a high proportion of dispersers may have unknown origins, even when the number of home ranges moved is relatively small. Initially, this seems surprising. However, the result is logical if one considers the number of prides that would lie within three home ranges of the edge of a large study site.

Many authors (Koenig *et al.* 1996) argue that genetic data often fail to correlate with observed patterns of dispersal clearly, despite the logical link between the two. This may be due to problems with empirical data collection or due to an imperfect understanding of the relationships between dispersal and genetic structure. Similarly, most authors agree that direct observations of dispersal are usually difficult to collect in sufficient numbers for a powerful and unbiased analysis. Koenig *et al.* (1996) concluded a recent review of dispersal distances by saying that 'the day that small PIT-like tags can be tracked by satellite will be the day we are finally able to obtain unbiased estimates of dispersal distributions in vertebrates' (p. 517). Our analysis shows that, for some species, the answers may come from microsatellites not satellites.

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