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REPORT

Genotyping faeces links individuals to their diet

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Abstract

The detection of individual variation in foraging behaviour within wild mammal populations requires large sample sizes and relies on the multifold re-sampling of individuals. However, limits for observational studies are posed by the rarity and nocturnal or otherwise elusive habits of many mammals. We propose that the detection of foraging variation within populations of mammals may be facilitated if conventional diet analysis from faeces is combined with DNA-based individual identification methods using "genetic fingerprinting" from faeces. We applied our approach to a coyote (*Canis latrans*) population, and showed how individuals may vary from one another in their diet profiles. Two main groups of coyotes were distinguished on the basis of their relative use of small mammals and "other vertebrates" as primary food sources, and these two groups were further subdivided on the basis of their relative use of "other vertebrates" and fruit as secondary food sources. We show that, unless a faecal sampling scheme is used that maximizes the number of different individuals included in a survey, individual foraging variation that is left unaccounted for may result in downwardly biased faecal diet diversity estimates. Our approach allows the re-sampling of individuals over time and space, and thus may be generally useful for the testing of optimal foraging theory hypotheses in mammals and also has conservation applications.

Keywords

Canis latrans, coyote, faeces, foraging behaviour, molecular scatology.

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INTRODUCTION

Studies of foraging behaviour serve important roles in the understanding of animal ecology, evolution and conservation (Sih 1993). In mammals, to obtain large sample sizes, and to bypass lengthy observational studies of often elusive and nocturnal animals, food habits are frequently assessed through the identification of food remains from faeces (Putman 1984). Such studies generally yield estimates of the average food preferences of the study population, and therefore may not be well suited to detect whether individuals vary in their preferred foods (Litvaitis 2000). Alternative foraging strategies, however, may result in fitness differences between individuals within populations (e.g. Ritchie 1991; Grant & Grant 1996). Consequently, the data are of limited value when, for example, optimal foraging theories are tested, intraspecific resource partitioning is examined or the concise food requirements of precious individuals of highly endangered populations are assessed.

In this report, we draw attention to a combination of two approaches that has the potential to uncover individual food preferences in mammals. This combination consists of conventional faeces-based diet analysis and the analysis of faeces with DNA-based individual identification methods using "genetic fingerprinting". This approach has been stimulated by a number of recent studies which have shown that the species, sex and identity of an animal can be deduced by the genetic analysis of its faeces with adequate DNA markers (e.g. Kohn & Wayne 1997). Of particular relevance is the fact that individuals in a population can be distinguished on the basis of their unique genotypes comprised of several microsatellite loci (multilocus genetic fingerprints) that can be obtained from their faeces by polymerase chain reaction (PCR) technology (Reed *et al.* 1997; Taberlet *et al.* 1997; Gerloff *et al.* 1999; Kohn *et al.* 1999). Thus, we propose that faeces, whose food content has been identified by conventional diet analysis, can subsequently be assigned to individuals identified through the genetic fingerprinting of the same faeces, and this approach may uncover hidden individual variation in diets. With this approach, large numbers of individuals can potentially be sampled several times and across the natural range of ecological conditions encountered during their

lifetime, and remains of food items in faeces can be identified at a fine taxonomic level. This non-invasive approach may therefore represent a significant advancement over methodologies that require the sometimes difficult or controversial capture of animals or that require animals to ingest bait (Crabtree *et al.* 1989; Bekoff & Jamielson 1996), or over other methods that rely on sporadic observation or sampling, e.g. the analysis of carcasses (Putman 1984; Litvaitis *et al.* 1986; Hiderbrand *et al.* 1996).

To examine the potential of a combination of diet analysis and molecular scatology to uncover individual foraging behaviour, we studied the food habits of a population of coyotes (*Canis latrans*) from the Santa Monica Mountains, California, U.S.A. (Kohn *et al.* 1999; Fedriani *et al.* 2000, 2001; Sauvajot *et al.* 2000). Conventional diet analysis from faeces has shown that the resident coyotes rely mainly on small mammals as food and, to a lesser extent, on other vertebrates, fruit, invertebrates and trash (Fedriani *et al.* 2000, 2001). This diverse diet of coyotes offers us an opportunity to examine if, and how strictly, each individual adheres to the average population diet profile. For this, we analysed and quantified the food composition of a collection of faeces that we had recently been able to assign to individual coyotes by "genetic fingerprinting" (Kohn *et al.* 1999). The dietary habits of mammals are often deduced from faecal analyses that do not account for individual variation. Therefore, we explored, by means of simulation, how such variation may skew estimates of population diets and how sampling schemes can minimize skew while maximizing sampling efficacy.

METHODS

Sampling and genotyping procedures

We collected 238 coyote faeces during a 2-week period in July 1997 along six transects that traverse an area of $\sim$15 km^2 in the Santa Monica Mountains of California (Kohn *et al.* 1999). A field experiment that measured the persistence time of faeces on trails and roadways, where the faeces were collected, has shown that they represent a time window of about 12 weeks (95% CI: 9–17) (Kohn *et al.* 1999). Genetic typing for the assignment of faeces to individuals used the three canid-specific microsatellite loci with locus and GenBank accession numbers (in parentheses): FH2001 (L78573 and L78574), FH2062 (L78593 and L78594) and FH2140 (L78623 and L78624) (Francisco *et al.* 1996; Mellersh *et al.* 1997). Typing of 115 out of 238 faeces was successful and resulted in 30 unique genotypes, all of confirmed coyote origin; the sex was determined for each of these using sex-specific probes (for molecular methods, see Kohn *et al.* 1999). The probability that any two genetic fingerprints were identical was 0.0065; thus, on average, in a population of about 154 animals, no two individuals are likely to share a genetic fingerprint. Using rarefaction analysis (Sanders 1968; Lehman & Wayne 1991; Hayek & Buzas 1997), the local population size was estimated as between 36 and 40 individuals (Kohn *et al.* 1999), and we assumed that the 30 unique genotypes represented a minimum of 30 individual coyotes. After completion of the DNA work, four of the 115 faeces were no longer useful for diet analysis, and these represented two coyotes. The study presented herein therefore utilized 28 coyotes represented by 111 faeces, and their identification numbers and sex are given in Table 1.

Diet analysis and statistics

The food remains of the faeces were analysed using standard methods (Reynolds & Aebischer 1991). Briefly, each identified food item was assigned to one of the five following categories: small mammals, "other vertebrates", invertebrates, fruit and trash. The relative abundance of food items belonging to each category in the faeces of a coyote was calculated and expressed as the percentage of occurrence (PO; Fedriani & Travaini 2000). PO was calculated as the number of times an item belonging to a given food category occurred in the faeces of a coyote ($\times$ 100) divided by the total number of times items belonging to any category occurred in the faeces assigned to that coyote (total number of occurrences). In calculating the number of occurrences, all remains belonging to a given food category within a sample (faeces) were pooled and treated as a unit (Rose & Polis 1998; Farrell *et al.* 2000; Fedriani *et al.* 2000, 2001). MANOVA (SAS Institute 1990) was used on the arcsine-transformed PO values (Zar 1984) to test the null hypothesis that there were no overall differences in the consumption of different food categories between the 17 coyotes that were sampled three or more times (i.e. there was no heterogeneity in the relative use of different food categories). One-way ANOVAs were used to test for differences for each food category separately. Significance was evaluated after the sequential Bonferroni method had been applied (Rice 1989). When significant differences were found for particular food categories, an index of repeatability, r (i.e. the intraclass correlation index; Møller 1994), was used to estimate the variance explained by individual variation.

To evaluate whether the individual variation may be an artefact of limited sample size, and to estimate the statistical thresholds that identify groups of coyotes with similar diet preferences, cluster analysis based on a diet dissimilarity matrix was performed, followed by a bootstrapping procedure. Diet dissimilarity was calculated as 1 – Pianka's (1973) index of similarity. Clustering used the unweighted pair-group average method (Romesburg 1984). A bootstrapping

Table 1 Diets of individual coyotes in the Santa Monica Mountains of California as assessed by genotyping faeces in combination with conventional analyses of prey identification. For analyses, we only considered 17 individuals sampled three or more times, which appear in (a) and are sorted by the eight clusters identified in Fig. 1. Individuals sampled less than three times (b) are sorted by gender. The importance of different food items in the overall sample of each individual was estimated by percentages of occurrence (see "Methods" section). Because faeces may comprise more than a single food item, the number of occurrences is often higher than the number of faeces

(a) Individuals sampled more than three times

Food item	M A*	F J*	M W†	M P‡	M T‡	F Y‡	M F§	M AC§	F N§	F I§	M X¶	F C¶	M H**	M L**	M B††	F O††	F Q‡‡
Small mammals	45	66	52	37	30	47	55	50	60	50	30	43	60	46	34	13	17
Other vertebrates	0	0	12	23	20	24	33	37	30	50	31	28	0	8	66	75	41
Invertebrates	18	33	18	27	30	24	11	0	0	0	4	0	0	8	0	0	33
Fruit	36	0	18	0	0	0	0	12	10	0	25	29	40	31	0	12	8
Trash	0	0	0	14	20	6	0	0	0	0	11	0	0	8	0	0	0
No. of occurrences	11	3	17	29	10	17	9	8	10	10	28	7	5	13	6	8	12
No. of faeces	6	3	8	11	3	9	5	4	4	6	9	3	3	8	6	5	3

M, male; F, female.
Clusters: *1; †2; ‡3; §4; ¶5; **6; ††7; ‡‡8.

(b) Individuals sampled less than three times

Food item	M D	M K	M M	M S	M AA	M AB	F E	F G	F R	F U	F V
Small mammals	0	40	50	33	50	50	50	66	50	0	50
Other vertebrates	75	60	0	33	0	25	50	0	0	100	0
Invertebrates	0	0	0	0	0	0	0	33	50	0	0
Fruit	25	0	50	0	50	25	0	0	0	0	50
Trash	0	0	0	33	0	0	0	0	0	0	0
No. of occurrences	4	5	2	3	2	4	2	3	4	1	2
No. of faeces	2	2	1	1	1	2	1	1	2	1	1

M, male; F, female.

procedure was devised in FoxPro (1993) and employed to evaluate the 95-percentile statistical breakpoint that separates the groups (Jaksic & Medel 1990). For this, 100 stochastic re-assignments of the five food categories to each of the coyotes were performed. After each re-assignment, diet dissimilarity between all pairs of coyotes was computed, resulting in 13 600 pseudo-values. The determined 95-percentile corresponded to a dissimilarity index of 0.07. Accordingly, observed dissimilarity indices less than 0.07 were considered to be significant at $P < 0.05$ in a one-tailed test (Jaksic & Medel 1990).

Effects of variation on non-individual-based diet diversity estimation

Variation in diet choice potentially may skew estimates of overall population diet if such variation is left unaccounted for. To explore this question, the Shannon index of diet diversity (H'; Brower & Zar 1984) was calculated for random samples that were generated from our empirical data matrix of the 17 coyotes sampled three or more times (Table 1). In the first set of simulations, H' was monitored as a function of the number of faeces sampled, and considering two scenarios that differed in the number of unique individuals that were represented by a given number of collected faeces. First, we assumed that all collected faeces represented only a single individual. Second, we assumed that each faeces would represent a new, previously unsampled individual. Thus, we either minimized or maximized the number of individuals sampled given any number of collected faeces.

In a second set of simulations, we explored how comprehensively any individual needs to be sampled in order to approach the maximum diet diversity estimates given our empirical data matrix (Table 1). These simulations are related to those outlined above, but in this case we take into consideration that it is desirable to minimize sampling effort without sacrificing the accuracy of non-individual-based faecal diet surveys. Three scenarios were simulated. First, we assumed that each individual, n, was only represented by one faecal sample, i. Thus, for $i = 6$, for example, $n = 6$. Second, we assumed that a threefold

re-sampling of each individual was achieved, i.e. for $i = 6$ the corresponding $n = 2$. Finally, we assumed that a maximum re-sampling of each individual had occurred, i.e. for $i = 11$ the corresponding $n = 1$ (male P; Table 1), and, for the entire sample of 96 faeces, on average about 5.7-fold re-sampling of each of the 17 coyotes, had occurred.

Each simulation was run for 50 iterations to generate the plausible ranges of diet diversity given our empirical data (Table 1). In both sets of simulations, generalized linear models (GLM), implemented in PROC GLM (SAS Institute 1990), were used to compare values of diet diversity.

RESULTS AND DISCUSSION

Coyote diet profile and individual variation

Between one and 11 faeces per coyote were available for analysis (Table 1). Of these, three or more faeces were available for 17 of the 28 coyotes, totalling 96 faeces, corresponding to a mean of 5.65 faeces per individual, and we focused on these during subsequent analyses (Table 1). Thus, we studied the food preferences of between 43% and 47% of the estimated 36–40 coyotes residing in the study area at the time of collection (Kohn *et al.* 1999).

Analysis recovered 203 different items that could be classified into one of the five specified food categories (Table 1). The remains of small mammals were found in the faeces of all 17 coyotes and accounted for 43 ± 4% (1SE) of all items identified. "Other vertebrates" occurred in the faeces of 14 coyotes, and made up 28 ± 5% of the total items (Table 1). Fruit and invertebrates were consumed by 10 coyotes, accounting for 12–13% of the total items (Table 1). This diet profile was similar to that found in the coyotes that were sampled fewer than three times (Table 1), and was also in agreement with our previous survey that utilized 761 coyote faeces (Fedriani *et al.* 2000), suggesting that sampling drift is of limited effect.

The inclusion of information on individual identities, as determined by the genetic fingerprinting of faeces, revealed a significant heterogeneity of diet profiles (MANOVA; $F = 1.71$, d.f. $= 80$, $P = 0.0005$). Cluster analysis based on diet dissimilarity suggested the existence of two main groups of coyote, I and II, that differed by a dissimilarity index of 0.25 (Fig. 1). Group I consisted of 14 (82%) individuals (A, J, W, P, T, Y, F, AC, N, I, X, C, H and L) and, in this group, small mammals accounted for the largest proportion (30–66%) of food items (Table 1). In contrast, in the smaller group II comprising only three (18%) coyotes (B, O and Q), "other vertebrates" were the main (41–73%) food item (Table 1). In agreement with diet estimates that were derived without the knowledge of individuals (Fedriani *et al.* 2000), the majority of coyotes in the study area thus relied on small mammals as the primary food source, and conclusions from non-individual-based scatology surveys concerning the primary food may therefore be generally robust. However, 18% of the sampled coyotes deviated in their primary food choice, and this fraction will be missed in studies that do not take individual variation into account.

Variation in the preferred secondary food sources further divided individuals into smaller clusters, 1–8, that significantly ($P < 0.05$) differed from one another by a dissimilarity index of 0.07 (Fig. 1). Group I, which relied on small mammals as the main food source, was subdivided on the basis of the relative importance of the secondary foods "other vertebrates" and invertebrates (e.g. cluster 1 vs. cluster 5) or invertebrates and trash (e.g. cluster 3 vs. cluster 4). Significance analysis showed that, of the five food categories, only the choice of "other vertebrates" (ANOVA; $r = 0.28$, $F_{16,79} = 3.14$, $P < 0.01$) and

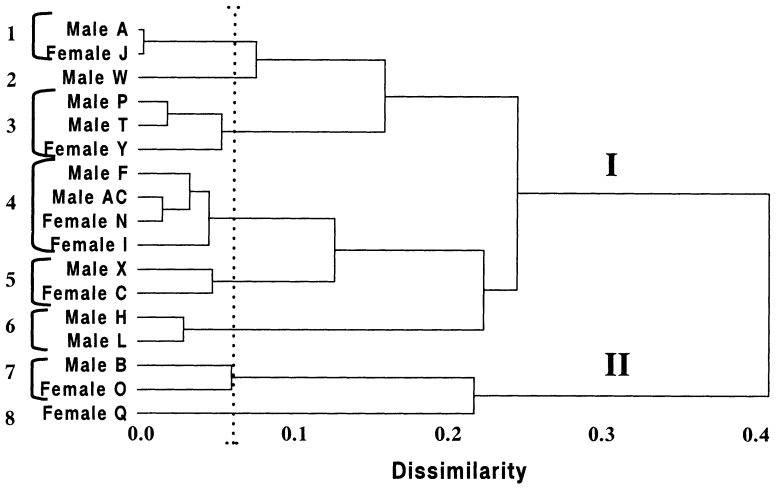

Figure 1 Clustering of coyotes based on diet dissimilarity. Two main clusters that differ by a dissimilarity index of 0.25 are denoted as I and II, and these differ in their primary use of small mammals and other vertebrates, respectively (Table 1). There is further subdivision of clusters into subclusters, denoted 1–8, which differ significantly ($P < 0.05$) by a dissimilarity index of 0.07 (broken vertical line).

fruit ($r = 0.19$, $F_{16,79} = 2.30$, $P < 0.05$) as secondary foods contributed to the heterogeneity of diet profiles, and indexes of repeatability indicated that 28% and 19%, respectively, of the variance was explained by their differential consumption. As with estimates of primary food sources, individual variation in the prevalence of the secondary food source is not accounted for in average estimates of diet.

It is unclear whether the pattern of variation would persist if a survey was conducted that spanned a longer time-scale than ours. However, variations in the foraging behaviour of coyotes have been reported from longer term field studies, and these have revealed some ties to social ecological factors of coyotes (Bekoff & Wells 1980, 1981; Bowen 1981; Gese *et al.* 1996a,b; Shivik *et al.* 1996). In addition, quantitative and qualitative differences in food resource usage have been shown to be a causative agent underlying locally enhanced coyote densities (Bekoff & Wells 1980; Fedriani *et al.* 2001). Thus, conceivably, our reported statistical signal of diet profile heterogeneity may have an underlying biological significance that needs to be examined by further fieldwork, which may be effectively assisted by our approach.

Potential downward bias in diet diversity estimates of non-individual-based surveys

To evaluate whether our estimates of overall population diet could potentially be skewed if individual variation is left unaccounted for, we performed two sets of simulations and monitored diet diversity (H') as a function of the number of examined faeces (see "Methods" section). The results from our first set of simulations (Fig. 2A) indicated that diet diversity of individuals is only a subset of that of the entire population, and thus diet diversity estimates derived from faecal collections that represent many unique individuals always significantly exceed those estimates derived from faecal collections that only represent a single individual (GLM, $F = 11.56$, d.f. $= 1$, $P = 0.0007$). This result suggests that non-individual-based diversity indices may be downwardly biased when the faeces collection represents a small number of redundantly sampled individuals, and the bias is reduced when large faecal collections are considered.

In a second set of simulations, it was estimated how many times individuals should be re-sampled to obtain a reliable picture of the average population diet during non-individual-

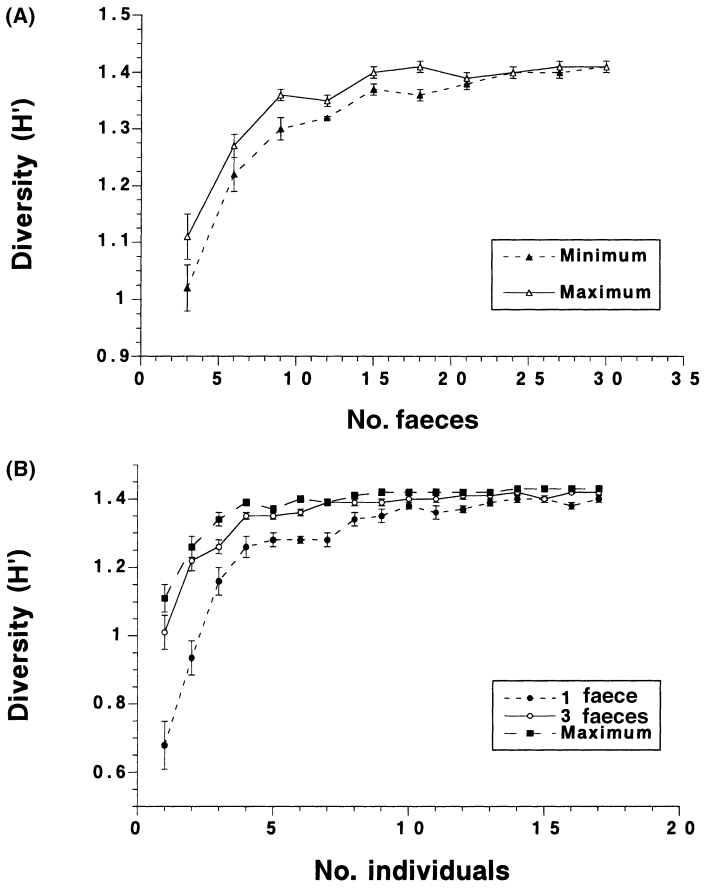

Figure 2 Diet diversity, H', of randomly generated samples plotted vs. the number of faeces (A) and the number of individuals sampled (B). (A) Diet diversity when the number of individuals sampled was maximized (full line, open triangles) and minimized (broken line, filled triangles). (B) Diet diversity for maximum possible re-sampling (filled squares), three-fold re-sampling (full line, open circles) and one-fold re-sampling (broken line, filled circles) of each individual.

based surveys (Fig. 2B). Analysis required that the effect of faecal collection size on diet diversity (GLM, $F = 305.0$, d.f. $= 1$, $P < 0.0001$) was controlled for. Then, diet diversity was significantly higher for faecal collections representing at least three-fold re-sampled individuals ($F = 112.5$, d.f. $= 2$, $P < 0.0001$). However, maximizing the number of faeces per individual had little effect on overall diet diversity estimates (Fig. 2B), suggesting that there is little within-individual, faeces-to-faeces variation in the simulated dataset. Thus, the significant indices of repeatability computed for the empirical data matrix (Table 1) are unlikely to be an artefact of a small sample size, and our three-fold re-sampling of each coyote is probably appropriate to examine whether individual variation in diet exists. Finally, these simulations show that, in our study population, diet diversity generally exceeds individual diet diversities.

These simulation results may provide some guidance when large-scale and long-term monitoring programmes are planned that may lead to extensive sampling and laboratory analyses. To minimize effort without sacrificing accuracy, faecal collection programmes should aim to achieve a multiple-fold re-sampling of individuals, and ensure that a large number of individuals is included in the survey (Fig. 2A, B). However, we caution that sampling considerations intrinsic to our particular study system and also to non-invasive genotyping, where not every sample yields DNA suitable for analysis (Taberlet *et al.* 1996; Frantzen *et al.* 1998), need to be explored on a case-by-case basis.

CONCLUSIONS

In this report, we used a previously unexplored combination of conventional diet analysis from faeces and genetic fingerprinting methods that allow us to assign faeces to individual coyotes in the study population. Using this combined approach, significant differences in the relative use of different food resources by coyotes emerged that were not apparent during a previous non-individual-based faecal survey. Such individual differences in foraging tactics potentially contribute to the population variance in fitness that may be tied to lifetime reproductive success (Ritchie 1991; Grant & Grant 1996). Testing such hypotheses requires detailed field studies over relevant spatial and temporal scales however (e.g. Clutton-Brock 1988), and we suggest that diet analysis of genetically tagged faeces may assist such studies. Our approach may also be relevant to conservation by assisting to estimate the extent to which changes in prey availability will impact demographic parameters of, often sensitive, predator populations (Weaver *et al.* 1996).

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BIOSKETCH

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