DO INDIVIDUAL DIFFERENCES INFLUENCE FLIGHT INITIATION DISTANCE?

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Abstract: Flight initiation distance (FID), or the distance between a prey animal and an approaching intruder when the prey initiates its escape, is an important factor in wildlife management. We conducted a study on individually identified yellow-bellied marmots (*Marmota flaviventris*) to test 3 key assumptions of FID research: (1) differences in individual responses are small enough so as not to confound results; (2) pseudoreplication may bias results; and (3) habituation and sensitization can be studied without knowledge of individuals. We found that individual identity was not a significant predictor of FID. Furthermore, a moderate degree of pseudoreplication did not significantly affect the results of most analyses. However, individuals differed greatly in their rates of habituation, such that habituation was apparent only when individual identity was known and could not be detected without knowledge of individuals. If our marmot results can be generalized to other species, they suggest that researchers need not be concerned about individual identity when studying variables largely dependent on environmental factors, but that identification of individuals is important for studies of properties of individuals, such as habituation.

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Behavioral studies have demonstrated systematic differences among individuals, age classes, and sex classes in how animals assess predation risk (Lima and Dill 1990; Frid and Dill 2002). Because of the importance of individual variation in explaining patterns of behavior (Wilson et al. 1994), behavioral biologists and ecologists have been justifiably concerned with keeping track of individuals to avoid pseudoreplication (Hurlbert 1984) and data pooling (Machlis et al. 1985). Leger and Didrichsons (1994) examined the statistical consequences of combining observations from the same individual and reported that pooling did not affect results when intra-subject variance was greater than inter-subject variance. However, if individual identities are unknown, then researchers cannot determine whether this criterion is met.

Flight initiation distance (Ydenberg and Dill 1986), also called "flush distance" (Holmes et al. 1993) and "escape flight distance" (Madsen and Fox 1995), is the distance between a prey animal and an approaching intruder when the prey animal begins its escape. Although the magnitude of individual effects on FID has not been studied, many FID studies do attempt to avoid pseudoreplication. For individuals associated with a particular location, such as a burrow or a nest, burrow location can be a useful way to identify individuals. For example, Bonefant and Kramer (1996) identified individuals by their burrows and used only 2 observations/individual. Blumstein et al. (2001) used individually marked animals, natural variation in pelage, or location to avoid sampling individuals more than once. However, many species are found in aggregations or are otherwise not associated with a specific location. In these cases, sampling different locations is the only way to avoid pseudoreplication if subjects are neither marked nor otherwise individually identifiable (e.g., Blumstein and Daniel 2002, Blumstein et al. 2003).

Despite researchers' efforts, some degree of pseudoreplication might be unavoidable, and understanding the degree that having more than a single observation per individual influences results of FID research is essential. We studied individually identified yellow-bellied marmots to test the following key assumptions of most FID research: (1) differences among individual responses are small enough so as not to confound results; (2) pseudoreplication (i.e., having >1 sample/individual) may bias results; and (3) habituation and sensitization can be studied without knowledge of individuals.

METHODS

Study Organism and Site

Yellow-bellied marmots are 2–6-kg social, sciurid rodents (Frase and Hoffmann 1980). They

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live in social groups in subalpine areas, often occupying burrow networks on steep slopes (Armitage 1991). Burrows are usually excavated under large rocks for protection from burrowing predators; however, marmots also live in flat, grassy, or nonrocky areas (Svendsen 1976). Marmots escape to their burrows to avoid predators (Blumstein 1998; Blumstein et al. 2001).

We conducted our study between May and July 2003 at the Rocky Mountain Biological Laboratory in Gothic, Colorado, USA (38°57′N, 106°59′W). We studied marmots at the following colony sites: River, Bench, Marmot Meadow, Picnic, and Stonefield (Armitage 1991)—areas with human visitation but not cohabitation.

Data Collection

As part of an ongoing study, we experimentally flushed 39 marmots, which had been marked with nontoxic Nyanzol dye symbols enabling identification from distances ≤400 m (Armitage 1982). Because marmots sometimes became alarmed when we arrived at a site, we quietly observed the site for at least 5 min after arrival. During this observation period, we identified marmots with a 15–45X spotting scope. After selecting a marmot for testing, the researcher stood and walked directly toward the focal marmot at a speed of 1 0.5-m step/sec. To avoid variation caused by having multiple observers, a single researcher (A. Runyan) performed all FID trials. The observer maintained the same speed and posture when approaching a marmot and made note of the pace number at which the marmot first moved (to compute FID). We also recorded the number of paces from the researcher's initial location to the marmot's initial location and the number of paces from the marmot's first location to escape location. Paces were converted to meters for analysis. We calculated FID by subtracting the distance at which the marmot first moved from the total distance the researcher walked.

Data Analysis

We fit general linear models to the data using SPSS 10 (SPSS 2000). Because starting distance has an important effect on FID in many species (Blumstein 2003), we included starting distance as an independent variable in every model. We fit 2 models to explain variation in FID: (1) starting distance and individual identity; and (2) starting distance, individual identity, and the interaction between individual identity and starting distance. We forced models through the origin because a starting distance of zero should yield an FID of zero. For those models testing individual effects, we needed >1 observation/individual. We used 2 different samples for these models: (1) 5 marmots tested ≥5 times, and (2) 9 marmots tested ≥3 times.

We performed several bootstrap simulations to compare the results we obtained with those we might have reported had we not known the identities of the studied individuals. In the first simulation, we compared the results of an analysis of variance (ANOVA) performed on 25 different nonpseudoreplicated datasets created by randomly choosing 1 of the observations obtained for each of the 39 individuals. Because 24 individuals were observed only once, these 24 observations were present in all of the datasets. This simulation represented the results researchers might obtain if they completely avoided pseudoreplication.

The second simulation approximated the results we might have obtained had we not known the identities of individuals, as is the case in most ecological studies. For this simulation, we randomly chose 25 sets of 39 observations from the set of all recorded observations. This yielded 25 different sample datasets chosen without regard for individual identity. Many of these datasets contained multiple observations from single animals, as would datasets in a study in which researchers did not attempt to use only 1 observation/animal.

The group of datasets with 1 observation/individual and the group of datasets of randomly chosen observations differed not only in whether they contained >1 observation/individual, but also in the similarity of datasets within a group. The nonpseudoreplicated datasets were more similar to one another than the randomly created datasets. This was because 24 individuals were observed only once, and these observations were present in each of the 25 datasets. We wanted 2 sample groups that differed in whether they were pseudoreplicated, but did not differ in the degree of similarity among datasets in the group. Therefore, we created 25 more datasets of 39 observations, this time randomly reassigning observations to identities and then selecting 1 observation/individual in exactly the same manner as for the nonpseudoreplicated datasets. That is, we randomly reordered the observations and then used the same selection matrix that had been used for the first nonpseudoreplicated sets (e.g., the first dataset consisted of the first, third, seventh, etc., observations, and so on). Thus, these "variance-controlled" pseudoreplicated

Table 1. Results from a linear model explaining variation in flight initiation distance of yellow-bellied marmots that was fit to individuals with ≥5 trials (adjusted R^2 = 0.878), Colorado, USA, 2003. Variation explained by model parameters also is given.

	P-value	Partial Eta-squared
Model	0.000	0.900
Intruder starting distance (m)	0.000	0.489
Individual identity	0.240	0.211

Table 3. Results from a linear model fitted explaining variation in flight initiation distance of yellow-bellied marmots that contained nonpseudoreplicated data (adjusted R^2 = 0.874), Colorado, USA, 2003. Variation explained by model parameters also is given.

	P-value	Partial Eta-squared
Model	0.000	0.880
Intruder starting distance (m)	0.000	0.802
Distance to burrow (m)	0.267	0.033

datasets, as well as the nonpseudoreplicated sets, contained 24 observations that were present in all 25 samples, 14 cases present in approximately half the samples, etc.

We used these 75 simulated datasets (3 groups of 25 each) to determine whether the initial distance of a marmot from its escape burrow influenced that animal's FID, as it does with woodchucks (*Marmota monax*; Bonefant and Kramer 1996). Thus, we fit 77 linear models with these data: an initial model with 1 observation/individual, 25 simulations using the 3 different data selection algorithms, and 1 model with all 83 cases in the dataset. Specifically, the models sought to explain variation in FID as a function of starting distance and the marmot's initial distance to a burrow. For individuals observed ≥3 times, we calculated the intra-class correlation coefficient (Sokal and Rohlf 1981:216) as a measure of repeatability.

To study habituation, we fit 3 general linear models to explain variation in FID. The first used a dataset consisting of 1 observation/individual and modeled FID as a function of intruder starting distance and the ordinal number of the trials. The second and third models focused on individuals tested ≥5 times. The second model included intruder starting distance and the ordinal number of the trials. The third model included intruder starting distance, the ordinal number of the trials, individual identity, and the interaction between ordinal number and identity. For the latter 2 analyses, we also plotted the residuals after controlling for starting distance against the ordinal number of trials.

Table 2. Results from a linear model explaining variation in flight initiation distance of yellow-bellied marmots that was fit to individuals with ≥5 trials (adjusted R^2 = 0.864), Colorado, USA, 2003. Variation explained by model parameters also is given.

	P-value	Partial Eta-squared
Model	0.000	0.905
Intruder starting distance (m)	0.160	0.050
Individual identity	0.941	0.084
Intruder starting distance * individual identity	0.871	0.050

Throughout, we interpreted $P < 0.05$ as significant and $0.05 \le P < 0.1$ as marginally significant. We report adjusted R^2 values and partial Eta-squares as measures of effect size. Residuals from linear models were visually examined for normality. No transformations were required to meet assumptions of these models.

RESULTS

Individual Identity

After accounting for variation explained by intruder starting distance, individual identity explained no significant variation in FID (Table 1). The interaction between individual identity and starting distance was also nonsignificant, which implies that individuals did not have fundamentally different responses to variation in starting distance (Table 2). Most of the variation in FID was a function of external context, rather than being a characteristic of an individual (intra-class correlation = 0.09).

Pseudoreplication Simulations

After accounting for significant variation explained by starting distance, no significant variation in FID was explained by the marmot's initial distance to the burrow (Table 3). All 3 simulations were consistent with this finding: the 95% confidence intervals for the *P*-values for the variable distance to burrow did not extend below 0.05. The 95% confidence intervals for the 3 sets were as follows: nonpseudoreplicated sets: 0.529 to 0.700; randomly created pseudoreplicated sets: 0.277 to 0.587; and variance-controlled pseudoreplicated sets: 0.188 to 0.423. With the entire dataset (83 individuals), the *P*-value for distance to burrow was 0.181. Thus, the same result—nonsignificance—was obtained with the pseudoreplicated and nonpseudoreplicated datasets.

Habituation

After explaining significant variation accounted for by intruder starting distance, ordinal trial number was not a significant predictor of FID (Table

Table 4. Results from general linear model explaining variation in flight initiation distance of yellow-bellied marmots that contained 1 observation/individual (adjusted $R^2 = 0.871$), Colorado, USA, 2003. Variation explained by model parameters also is given.

	P-value	Partial Eta-squared
Model	0.000	0.877
Intruder starting distance (m)	0.000	0.765
Ordinal trial number	0.848	0.001

4). However, habituation became apparent after accounting for individual differences. In a general linear model explaining variation in FID as a function of starting distance, trial number, individual identity, and the interaction of trial number and individual identity (to test for differential habituation among individuals), trial number, and, to a lesser extent, the interaction between trial number and individual, were significant (Table 5). To illustrate how knowledge of individuals is essential for studying habituation, we compared the overall fit line and overall habituation statistics with those of each individual tested ≥5 times (Fig. 1). Overall, we found no main effect of ordinal trial number on FID, but an interaction effect existed; individuals responded differently to repeated flushes.

DISCUSSION

For yellow-bellied marmots, our results suggest that individual identity does not explain significant variation in FID, which implies that FID is more a function of external conditions than a consequence of individual identity. This conclusion is supported by the relatively small intra-class correlation coefficient. From these findings, we conclude that pseudoreplication in FID studies will probably not affect the results. However, this is only true when the studied phenomena do not depend on individual identity; our findings suggest that individuals may habituate or sensitize differently. Therefore, to test for habituation, patterns of change may need to be tested for each individual.

Table 5. Results from a general linear model explaining variation in flight initiation distance of yellow-bellied marmots that was fit to individuals with ≥5 trials (adjusted $R^2 = 0.912$), Colorado, USA, 2003. Variation explained by model parameters also is given.

	P-value	Partial Eta-squared
Model	0.000	0.941
Intruder starting distance (m)	0.000	0.645
Ordinal trial number	0.021	0.219
Individual identity	0.423	0.190
Interaction of ordinal trial number * individual identity	0.087	0.299

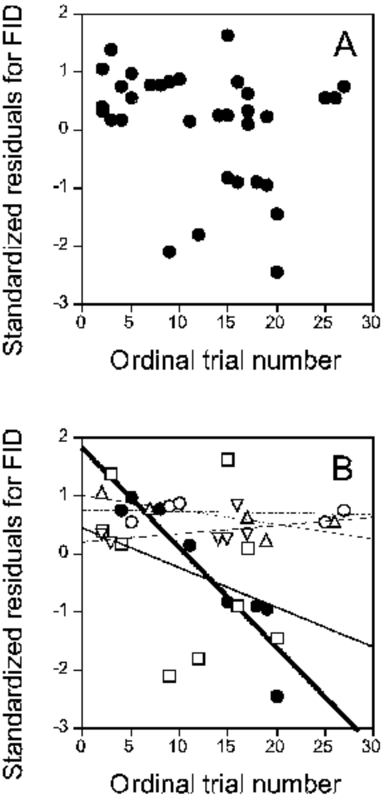

Fig. 1. (A) The residuals for flight initiation distance (after accounting for starting distance) for yellow-bellied marmots are not significantly correlated with the ordinal number of a trial ($r = -0.273$, $P = 0.124$, $n = 33$ all trials from individuals with 5 or more trials). (B) The relationship between ordinal trial number at a marmot site and residual flight initiation distance was influenced by marmot identity. All trials were conducted in Colorado, USA, in 2003.

Individual differences have been shown to explain much of the variation in antipredator behaviors such as general time allocation (Armitage et al. 1996) and overall "shyness" and "boldness" (Wilson et al. 1994). It is intriguing that FID, in contrast, depends very little on individual effects. Flight initiation distance possibly depends little on individual identities because individuals affect each others' FIDs—we often observed groups of marmots fleeing within seconds of each other (sensu Lima 1995).

MANAGEMENT IMPLICATIONS

Our finding that pseudoreplication does not necessarily affect the results of FID analyses are useful to wildlife managers seeking to study effects of humans or design buffer zones. For example, in our study, the pseudoreplicated data set was more than twice as large as the nonpseudoreplicated set. Assuming only a minor degree of pseudoreplication (i.e., researchers did not conduct all their flushes at a single location with a small population of subjects), then mangers need not worry about a moderate degree of pseudoreplication. By doing so, the statistical power of studies could be substantially increased by collecting all data possible. However, when studying effects that obviously depend on individual differences, such as habituation, or those that vary considerably among individuals, pseudoreplication should be avoided.

One option for determining which traits can be studied with a pooled dataset is to compare the results from many randomly chosen subsets. If these results are similar, then individual effects likely explain little of the variance in the studied trait, and data pooling is permissible. However, if the results are highly variable, then the trait variation (1) may be strongly influenced by individual identity, such that subsamples with different mixes of individuals yield different results (as might be found if habituation is important); (2) may have a small effect size, and studying the trait may require controlling for variables with larger effect sizes (possibly individual identity); or (3) may be due to unexplained environmental factors.

For instance, if animals are found at variable distances from some anthropogenic disturbance (e.g., an oil well, a trail or road, or a campground), the variation in distance could reflect variation in individual tolerances for disturbance. In such a case, tolerant individuals would be found closer to an impact while less tolerant individuals would be found farther from an impact. While data pooling would allow us to identify variation at the population level, studying individual tolerances would allow us to better manage the impact because we could then focus specifically on factors that explain individual variation (e.g., age, sex, prior experience).

Data pooling would be inappropriate if the variation were due to individual differences because unless the pooled sample contained equal numbers of trials from each individual, then the overrepresented individuals would bias the results. Pooling is permissible if the variation is mainly due to environmental factors. However, researchers cannot always determine whether the variance in the results is due to individual differences, small effect size, or environmental factors. Hence, we suggest that data pooling only be used when studying (1) variables not dependent on individual identity, or (2) variables for which similar results are obtained from many different subsamples of the data.

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