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SOURCES OF VARIATION IN MEASUREMENTS OF BIRDS IN A PUERTO RICAN DRY FOREST

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Abstract.—Based on more than 2000 total captures of 40 species of birds in 14 avian families, resulting from 15 yr of banding at a single net line in southwestern Puerto Rico, body mass and wing length measurements of 246 individuals of 25 species of birds that were captured and recaptured 612 times were used to show that: (1) Among and within different individuals, temporal variation in selected avian morphological characters is minimal when measurements are taken at the same time of year. (2) Measuring instruments widely used in the field are precise. (3) Sampling techniques are comparable. (4) Investigator influence, for single and cooperative banders, is minimal even when small samples are compared. Seasonal and daily variation within the data did appear, however, and were attributed to seasonal fluctuations of food resources, feather wear, breeding activities, and the added mass of ingested food. These data emphasize that the time of measurement is a critical factor when comparing morphological measures among different studies. Comparing measures from one season with those from another, or comparing measures taken during a whole year with those taken during a brief period, may show differences that are not biologically significant.

FUENTES DE VARIACIÓN EN LAS MEDIDAS DE AVES ESTUDIADAS EN UN BOSQUE XEROFÍTICO DE PUERTO RICO

Resumen.—Durante 15 años se han anillado aves en una localidad particular del suroeste de Puerto Rico. Datos sobre el peso y largo del ala de 25 especies de aves representados por 246 individuos que fueron capturados y recapturados en 612 ocasiones son utilizados para demostrar que: (1) entre diferentes individuos la variación temporal de características morfológicas son mínimas, cuando las medidas son tomadas durante la misma época del año; (2) los instrumentos usualmente utilizados en el campo para tomar medidas son precisos; (3) las técnicas de muestreo son comparables; (4) la influencia del investigador sobre anilladores particulares o en grupos, es mínima cuando se comparan muestras pequeñas. Variaciones diarias o estacionales fueron encontradas. Estas son atribuidas a factores tales como respuestas a las fluctuaciones en recursos alimenticios, desgaste de la pluma, actividades

reproductivas y al incremento en peso por ingestión de alimento. Los datos enfatizan que el tiempo en que se toman las medidas es crítico cuando se comparan parámetros morfológicos tomados en diferentes estudios. El comparar parámetros tomados en una estación del año con otros tomados en otra o el comparar medidas tomadas durante todo un año con otros de un breve periodo, pueden mostrar diferencias que no son biológicamente significativas.

Many studies in avian morphology address the variation of skeletal and plumage characters in an evolutionary (Selander 1971) or ecological context (Hespenheide 1973). When taking measurements of avian morphological characters in museums, exacting techniques can be used. However, measuring birds under the rigors of field conditions is more difficult, and biologists often question the accuracy of the data generated. Such uncertainty is increased when data are gathered by more than one person (i.e., investigator influence). In laboratory studies, Berger (1968), Collins and Atwood (1981) and Nisbet et al. (1970) showed that field scales, spring balances, and calipers used widely to measure avian body mass and wing chord are accurate and that investigator influence does not appear when working with large sample sizes. However, less is known about measurement accuracy under field conditions, especially among many workers dealing with small samples. In this study, morphological variation in Puerto Rican dry forest birds was examined over a 15-yr period that included severe drought conditions (Faaborg et al. 1984). Because numerous banders, often using dissimilar instrumentation, gathered these data at different times, the effects of investigator influence and banding techniques were analyzed to determine if they affected measurements of body mass and wing length in sampled birds.

STUDY AREA AND METHODS

Mensural data were collected from birds (vernacular and scientific names in the Appendix) captured over a 15-yr period (1973–1988) at our net line within the Guanica Forest located in southwestern Puerto Rico (see Terborgh and Faaborg 1973 for a description of netting techniques and the area). Most of the sampling was done during the dry season, January or early February of 1973–1976, 1978, 1980–1988. Some sampling was done during the wet season, June of 1973, and July of 1981, for comparison. All birds were weighed with Pesola spring scales, either in bags (WJA) or by their leg bands (JRF and his students). Wing chord (from the bend of the wing at rest to the longest primary) was measured with dial calipers (WJA) or with a wing rule (JRF and students). Although JRF et al. shared in taking body measurements during the first half of the study (1973–1980), and in 1988, WJA alone weighed and measured all birds during the second half (1981–1987) of the study, excluding 1988. Investigator influence involving biologists other than JRF and WJA is assessed for the first half of the study (1973–1980).

Both parametric and nonparametric statistical tests were used to analyze the data. An F-test showed homogeneous variance of both body mass and wing chord measurements between captures and recaptures in all species tested, justifying the assumption that the probability density func-

tions $F(x)$ and $G(x)$ take the same form. Because interspecific morphological characters were compared, the coefficient of variation (CV) for each species was used to standardize our measures among variform species. Interspecific coefficients of variation were compared using methods described in Lewontin (1966). Analysis of variance (ANOVA) and Student's t -tests were used in most body mass and wing chord comparisons. A repeated measures ANOVA test was used to compare wing chord and body mass differences between captures and recaptures of the same individuals banded by a single bander using the same instruments and techniques at each measurement. A nonparametric procedure, the Wilcoxon signed-rank test (testing median differences in paired samples), was substituted when paired sample sizes were small or when the form of the probability density functions was in doubt. Significance was assumed at the 5% level in all statistical tests.

RESULTS

Summary of captures and recaptures.—More than 2000 individual birds comprising 40 species in 14 avian families were captured between 1973 and 1988 at our Guanica netline. Of the 40 different species captured, 25 species were recaptured at least once. JRF, his colleagues, and his students captured birds over 7 seasons (1973–1976, 1978, 1980, 1988). Of 887 total captures during these years, 63 individuals of 17 avian species in 8 avian families were captured and recaptured 133 times, with each individual being captured an average of 2.3 times ($SD = 0.54$, range = 2–4, $CV = 0.2$). Interestingly, 744 (almost 84%) were never recaptured. During a similar 7-season sampling period (1981–1987), more than 1000 total captures were recorded by WJA and his groups, who captured 138 individuals of 24 avian species in 10 families a total of 329 times, with each individual being captured an average of 2.4 times ($SD = 0.83$, range = 2–6, $CV = 0.3$). Similarly, some 700 individual birds (about 70%) were never recaptured during this period. During the entire 16-season sampling period, some birds were captured and recaptured one or more times by JRF et al. (1973–1980) and then later recaptured one or more times by WJA et al. (1981–1987), or vice versa (1988). This resulted in a total of 45 individuals of 13 species in 7 families that were captured a total of 140 times, with an average capture rate of 3.1 per individual ($SD = 1.26$, range = 2–7, $CV = 0.4$). Bananaquits, Puerto Rican Bullfinches, and Puerto Rican Flycatchers made up about 50% of JRF et al.'s captures and recaptures, and about the same percentage in JRF et al.'s captures and WJA et al.'s recaptures, whereas bananaquits, bullfinches, and Pearly-eyed Thrashers constituted about 50% of WJA et al.'s captures and recaptures.

Temporal variation.—In adult birds, intraspecific body mass and size, though geographically variable (Baker 1980), are fairly constant locally. However yearly, seasonal, and even daily differences have been reported for species and individuals in restricted geographic areas; see Clark (1979) for a review, and Biermann and Sealy (1985). To compare intraspecific

variation in size, measurements of body mass and wing (chord) length were taken on the 11 most common species captured at Guanica (see Appendix). Intraspecific coefficients of variation (CV's) for wing chord ranged from 2% in the Black-and-white Warbler to 6% in the Puerto Rican Tody. CV's for body mass ranged from 5% in the Red-legged Thrush to 12% in the bullfinch. Larger CV's for body mass may reflect the inclusion of some juvenile individuals in the more monochromatic species and daily mass fluctuations. Fluctuation in body mass on a daily and hourly basis is due, at least in part, to such factors as food intake, long flights (e.g., migration), fluctuations in ambient temperatures, lipid storage, and changes in the mass of internal organs (Fisher and Bartlett 1957, Gwinner 1975, Hussell 1969, Ioalé and Benvenuti 1982, Ketterson and Nolan 1978, Kontogiannis 1967, MacMillen and Carpenter 1976, Nice 1938, Odum 1949, Peterson 1972, Snow and Snow 1963, many others). To confirm or refute the possibility of daily fluctuations in body mass as a causative factor behind the observed 12% CV in the body mass of the bullfinch, we compared dry season hourly body masses of adult bullfinches, excluding summer samples and juveniles to avoid seasonal variability and possible age differences. Hourly body masses from 0600 to 1800 of 240 adult bullfinches (20 individuals in each of 12 hourly samples) were compared using analysis of variance procedures. There were no significant differences ($F = 0.548$, $df = 11,228$, $P > 0.05$) among any of the 12 hourly mean body masses ($\bar{x} = 31.69$ g, range = 30.75–33.07). Although there were no apparent hourly fluctuations in bullfinches, we did find hourly fluctuations in a larger (100 g) species, the Pearly-eyed Thrasher. Data were analyzed for two allopatric thrasher populations: the El Yunque highland (northeastern interior), wet forest population and the Guanica lowland, dry forest population. Mean hourly body mass was compared among three groups: (1) Guanica sexes lumped, (2) El Yunque sexes lumped, and (3) El Yunque sexes separated. Hourly body mass fluctuated similarly, not only in both dry and wet forest individuals, but also between sexes of the wet forest individuals (Fig. 1). There were slight body mass peaks at 1100 and 1500. Sample sizes of thrashers captured before 0700 were small at both banding sites and, therefore, the data were not included in Figure 1. However, the few thrashers that were captured before 0700 in El Yunque and at Guanica (6 and 9 individuals, respectively) were heavier (112 g and 99 g, respectively) than individuals captured between 0700 and 0800, suggesting that there are peaks in body mass about every 5 h (0600–1100) early in the day, and then every 4 h (1100–1500) later in the day. These data are consistent with extensive data on foraging behavior of wet forest thrashers taken from observation blinds (Arendt, unpubl. data). Wet forest thrashers forage heavily at dawn, then again just before mid-day, with another peak in mid-afternoon. As noted in Figure 1, highland, wet forest thrashers are heavier than lowland, dry forest individuals.

Temporal variability in body mass and size of adult birds is best evaluated using paired data from the same individual birds captured and

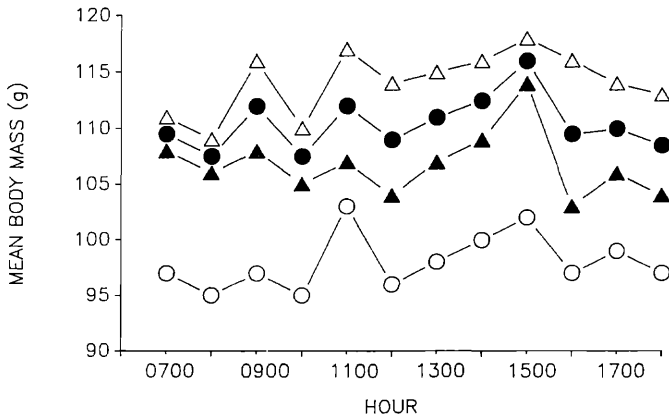


FIGURE 1. Comparison of hourly variation in body mass between adult Pearly-eyed Thrashers inhabiting the Guanica dry forest (sexes lumped ○) and the El Yunque wet forest (sexes lumped ●, males ▲, and females △).

recaptured over many years. During the past 15 yr at the Guanica study site, a few birds have been captured four or more times. Twenty-six individuals of ten species have been captured 123 times, with a capture rate of 4.7 per individual (SD = 0.91, range = 4–7) (Table 1). In individual birds that have been captured and recaptured over a period of many years and undergone repeated measurements, body mass and wing chord often vary only one or two grams or millimeters, respectively (Table 1). Two specific examples are given to illustrate this point. A Puerto Rican Tody (band no. 2-3310) has been captured and recaptured five times over a 14-yr period (1974–1988) (Table 1). Differences in the measurements of its body mass averaged half a gram and in wing chord about half a millimeter. When JRF initially captured it in 1974, body mass measured 5.2 g and its wing chord measured 42 mm. Fourteen years later, after being recaptured 3 additional times in the interim by WJA and JRF (with almost identical measurement results), it was once again recaptured by JRF. Its body mass and wing chord measured 5.8 g and 42 mm, respectively. Because larger-bodied birds often vary more in repeated measures of size and mass, a second example is offered. A Puerto Rican Flycatcher (band no. 3-4635) was captured and recaptured six times over a span of 11 yr (Table 1). During that period, differences in the measurements of its body mass averaged about half a gram and about a millimeter for its wing chord.

To eliminate possible confounding effects of different measuring devices and investigator influence in our temporal analyses, we compared body mass and wing chord length via repeated measurements of the same birds over time by a single bander using the same instruments and measuring techniques. A Student's paired *t*-test was conducted to compare temporal variability in mean body mass and wing length between initial captures ($n = 129$) and recaptured individuals ($n = 175$) of 24 species measured

TABLE 1. Body mass and wing chord differences of 26 individuals of ten species captured and recaptured 123 times from 1973 to 1988 in the Guanica Forest, southwestern Puerto Rico.

Species and band number	n	Capture years	Body mass (g)			Wing chord (mm)		
			\bar{x}	SD	$\bar{d}_{\text{min-max}}$	\bar{x}	SD	$\bar{d}_{\text{min-max}}$
Bananaquit (26)								
1700-55099	5	85, 85, 85, 86, 87	0.5	0.46	0.2-1.2	0.3	0.47	0-1.0
2-5411	5	78, 80, 81, 81, 82	0.2	0.18	0-0.7	2.8	1.35	0-4.1
2-5436	4	80, 81, 82, 83	0.2	0.15	0.1-0.4	2.1	1.25	1.3-3.6
2-5457	4	80, 81, 82, 84	0.3	0.43	0-0.8	3.1	1.40	1.7-4.5
118-24805	4	83, 83, 84, 85	0.2	0.20	0-0.4	2.9	1.00	1.9-3.9
118-24895	4	84, 84, 85, 86	0.2	0.15	0.1-0.4	0.4	0.36	0-0.7
Puerto Rican Bullfinch (26)								
1301-92412	5	82, 83, 84, 85, 85	1.6	1.35	0.4-3.3	2.2	1.61	0.6-4.4
4-3841	5	78, 80, 81, 82, 82	0.8	0.54	0.8-1.5	2.1	1.15	0.2-2.9
4-1096	4	73, 73, 74, 75	2.6	0.80	1.8-3.4	1.5	0.50	1.0-2.0
4-3843	4	80, 81, 82, 87	1.7	1.53	0-3.0	2.1	1.64	0.9-4.0
4-3848	4	80, 82, 84, 86	0.7	0.83	0.1-1.7	1.3	1.80	0.1-3.4
1351-35016	4	86, 86, 86, 87	1.0	0.75	0.3-1.8	0.4	0.69	0-1.2
Puerto Rican Flycatcher (17)								
3-4001	7	74, 75, 76, 78, 81, 81, 82	1.0	0.83	0.1-2.0	1.6	1.30	0.3-3.2
3-4635	6	76, 83, 83, 87, 87, 87	0.4	0.49	0-1.1	1.1	0.54	0.5-2.0
860-02804	4	81, 81, 85, 85	0.4	0.20	0.2-0.6	2.0	0.83	1.1-2.6
Puerto Rican Vireo (11)								
2-5431	7	78, 80, 80, 82, 86, 86, 86	0.9	0.53	0.2-1.7	1.4	1.28	0-3.0
2-5442	4	80, 81, 82, 84	0.5	0.26	0.3-0.8	0.1	0.05	0-0.1
Red-legged Thrush (11)								
592-44917	6	85, 85, 86, 86, 86, 88	2.4	1.05	1.5-3.5	2.0	1.82	0-4.0
592-44905	5	82, 82, 82, 83, 85	2.0	1.12	0.5-3.1	0.6	0.70	0.1-1.6
Puerto Rican Tody (10)								
118-24813	5	83, 84, 85, 86, 87	0.37	0.27	0.1-0.7	0.6	0.57	0.1-1.1
2-3310	5	74, 81, 81, 83, 88	0.57	0.28	0-0.9	0.4	0.31	0-0.7
Pearly-eyed Thrasher (9)								
1163-17802	5	81, 83, 85, 86, 86	1.4	1.10	0.9-3.1	3.0	1.48	0.5-3.7
5-1919	4	78, 80, 81, 85	1.5	2.15	0-4.0	2.2	2.04	0-4.0
American Redstart (5)								
124-44548	5	82, 82, 83, 84, 85	0.4	0.31	0.1-0.8	3.2	2.30	0.6-5.6

TABLE 1. Continued.

Species and band number	n	Capture years	Body mass (g)			Wing chord (mm)		
			\bar{x}	SD	$\bar{d}_{\text{min-max}}$	\bar{x}	SD	$\bar{d}_{\text{min-max}}$
Black-and-white Warbler (4)								
122-74839	4	81, 81, 81, 82	0.5	0.41	0.2-0.4	0.9	1.19	0.1-2.3
Adelaide's Warbler (4)								
2-5418	4	78, 80, 82, 83	0.6	0.32	0.6-1.8	1.8	1.20	0.3-3.0

only by WJA during the second half of the study (excluding 1988). No statistical differences were found between measurements of body masses ($t = 0.304$, $P = 0.759$, paired-sample t -test) and wing chords ($t = 0.943$, $P = 0.652$, paired-sample t -test) of captured and multiple-recaptured individuals. Because body mass and wing length of adult birds were shown not to vary significantly over time, we could eliminate the temporal variable (possible mass and wing length variability caused by yearly lapses of time between measurements) from the analyses. To further quantify the small margin of error in repeated measurements of the same individual birds over time by a single bander, we compared species-specific coefficients of variation (CV) for both body mass and wing length. Not only were intraspecific CV's equal between captures and recaptures for both body mass ($CV_{\bar{x}} = 7$, $SD = 2$, range = 4-12) and wing length ($CV_{\bar{x}} = 4$, $SD = 1$, range = 2-6), statistical tests comparing interspecific coefficients (Lewontin 1966) for both body mass ($P_{\bar{x}} = 0.379$, $SD = 0.077$, range = 0.275-0.464) and wing length ($P_{\bar{x}} = 0.279$, $SD = 0.085$, range = 0.162-0.458) showed equal variance between captures and recaptures among all sampled species.

Investigator bias.—Once we showed that measurement error on the same individuals of many different species of birds is minimal over time for a single bander, we could compare the possible influence of different banders. We compared mean body mass and wing length differences between captures and recaptures of 10 of the 11 most commonly captured species (Appendix) among three different investigator groups: (1) JRF et al. captures and recaptures, (2) WJA et al. captures and recaptures, and (3) JRF et al. captures, with recaptures by WJA et al. There was no significant observer effect at the 5% level among different banders for either body mass ($F = 0.731$, $df = 2,390$, $P = 0.574$) or wing length ($F = 0.745$, $df = 2,390$, $P = 0.745$). As an illustrative example of minimal variation in body mass and wing length in an individual bird measured by two different banders many years apart, a North American migrant, a female American Redstart (band no. 122-63961), was banded by JRF on 3 Feb. 1974 and recaptured 7 yr later by WJA on 27 Jan. 1981. The bird's capture-recapture body mass and wing lengths were: 6.8 and 6.7 g and 61.0 and 62.1 mm, respectively. After 7 years of presumably annual molt and reproduction plus 14 round trips to the United States, this bird showed a variation in body mass and wing length of only 0.1 g and 1.1

mm, respectively, reported by two different banders. This is especially impressive when one considers the fact that individuals of this species and sex have been reported to vary from 6.7 g to 11.2 g ($n = 170$) in body mass (Dunning 1984) and from 56.0 mm to 65.9 mm ($n = 298$) in wing chord (Robbins 1964).

Seasonal variation.—Having shown that neither time nor influence of different banders caused significant differences in body mass and wing length measurements taken at the same time of year, we could evaluate the possibility of seasonal variation in selected morphological characters. Comparisons of body mass and wing chord were made between individuals of nine species that were captured in either January or February from 1972 to 1981 ($n = 319$ inds.) and recaptured during June 1973 or July 1981 ($n = 115$ inds.). Half the species were heavier in June–July than in January–February. However, except for two small insectivores, the Adelaide's Warbler and Puerto Rican Tody, there was no significant difference in mean body mass between January–February and June–July captures ($t = -0.117$, $P = 0.902$, two-sample t -test). In contrast, all wing chord lengths were shorter in June–July captures, and significantly so in about half of the sampled species ($t = 2.761$, $P = 0.039$, two-sample t -test).

Instrument influence and sample size.—Because of the different methods and instrumentation used in determining body mass and wing chord lengths of captured birds, we compared techniques to evaluate the possibility of potential measuring-device influence. If different banders use different measuring instruments, but get similar results, there is no influence caused by the instrumentation. We stress, however, that although there were no significant differences in dry season (January–February) wing chord lengths, WJA's recapture wing lengths using dial calipers were consistently shorter (21 of 23 comparisons) than JRF et al.'s groups which used a wing rule. The number of shorter wing lengths using dial calipers was significantly higher ($P < 0.05$, Wilcoxon signed-rank test), with wing measurements averaging 0.74 mm shorter ($SD = 0.820$). The previous nonparametric statistical test (Wilcoxon signed-rank tests) showed that variation in morphological characters can be quantitatively compared even when working with small sample sizes.

DISCUSSION

Our data show that measurements of birds captured in a Puerto Rican forest in the early dry season did not vary from year to year, despite the effects of fluctuating environmental conditions and varying personnel. Climatic conditions ranged from wet to very dry and bird populations varied nearly 3-fold (see Faaborg et al. 1984), yet shifts in body mass did not accompany either good or bad periods. Seasonal and daily variation did appear, however, undoubtedly in response to seasonal fluctuations in food resources, feather wear, breeding activities, and food intake (for a discussion on variation of body mass and possible causative factors, i.e., breeding, molting, and migration, in repeatedly captured birds over dif-

ferent seasons and years, see Biermann and Sealy 1985, and Payne 1969). Our analyses also show that differences in the people making the measurements and the equipment they used had little effect upon the data gathered.

It should be pointed out that the measurements taken were chosen both for their ecological importance and because they were simple with maximum consistency from person to person. Although the authors often worked separately, they had worked together to compare techniques. It is reassuring that these measurements seem to be so consistent from person-to-person and over long periods of time, often with as much as a year between measurements.

These data emphasize that the season of measurement is a critical factor when comparing morphological measures from other studies. Comparing measures from one season with those from another, or comparing measures taken during a whole year with those taken during a brief period may show differences that are not a reflection of individual differences. When comparing museum skins, we suggest that the date of capture be recorded with all measures and, ideally, that the relative position of the date to the breeding season or some other standard be noted. Within these constraints, it appears that wing chord and body mass data provide very consistent results. Any differences that appear can be analyzed for their biological significance.

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APPENDIX

Vernacular and scientific names of birds recaptured within the Guanica Forest.

Vernacular name	Genus and species
Common Ground-Dove	<i>Columbina passerina</i>
Key West Quail-Dove	<i>Geotrygon chrysia</i>
Mangrove Cuckoo	<i>Coccyzus minor</i>
Puerto Rican Lizard-Cuckoo	<i>Saurothera vieilloti</i>
Puerto Rican Screech-Owl	<i>Otus nudipes</i>
*Puerto Rican Tody	<i>Todus mexicanus</i>
Puerto Rican Woodpecker	<i>Melanerpes portoricensis</i>
*Caribbean Elaenia	<i>Elaenia martinica</i>
*Puerto Rican Flycatcher	<i>Myiarchus antillarum</i>
Gray-cheeked Thrust	<i>Catharus minimus</i>
*Red-legged Thrush	<i>Turdus plumbeus</i>
*Pearly-eyed Thrasher	<i>Margarops fuscatus</i>
*Puerto Rican Vireo	<i>Vireo latimeri</i>
Northern Parula	<i>Parula americana</i>
*Adelaide's Warbler	<i>Dendroica adelaidae</i>
*Black-and-White Warbler	<i>Mniotilta varia</i>
*American Redstart	<i>Setophaga ruticilla</i>
Prothonotary Warbler	<i>Protonotaria citrea</i>
Ovenbird	<i>Seiurus aurocapillus</i>
Hooded Warbler	<i>Wilsonia citrina</i>
*Bananaquit	<i>Coereba flaveola</i>
Stripe-headed Tanager	<i>Spindalis zena</i>
*Puerto Rican Bullfinch	<i>Loxigilla portoricensis</i>
Black-cowled Oriole	<i>Icterus dominicensis</i>
Troupial	<i>Icterus icterus</i>

*Most commonly captured species.