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Rare or elusive? A test of expert knowledge about rarity of Amazon forest birds

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ABSTRACT

Aim To offer a test of expert knowledge about rarity of twenty Amazon forest bird species following an approach that equates rarity with low site occupancy and formally accounts for imperfect species detection. We define ten pairs of closely related species, each pair with one hypothetically common and one hypothetically rare species. Our null hypothesis is that members of each pair have similar occupancy, with hypothesized differences due to detection errors alone.

Location A 1000-ha plot of primary rainforest in the central Brazilian Amazon.

Methods We visited each of 55 sampling sites multiple times per season for three field seasons and estimated the probability of site occupancy by each species following a maximum likelihood state-space approach that also estimates the probability that a species is present yet undetected at a site. To maximize detection and account for its variation, we employed three different sampling techniques while systematically training and testing observer's ability to recognize species.

Results Occupancy estimates agree with expert predictions in all but two species pairs and show no evidence of clear temporal variation in occupancy between sampling seasons. Detection probability had a positive relation with observer ability, a strong relation to time of day across species, and a strong relation with the use of playback for some species. Detection with point counts and with autonomous recorders varied between species pairs.

Main conclusions We reject the null hypothesis of equal occupancy within pairs, concluding that expert knowledge on species rarity is useful and worth eliciting. Our results replace qualitative ratings of rarity with statistical estimates of occupancy, establishing a reliable baseline for future comparisons. Besides illustrating the relevance of expert knowledge, this application to Amazonian birds illustrates a flexible approach that can be used for testing knowledge about rarity for a variety of species groups and spatial scales.

Keywords
Acoustic sampling, birds, detection, expert knowledge, occupancy, rarity.

INTRODUCTION

Anyone faced with a difficult decision should benefit from additional information; however, it is often the lack of information that makes the decision difficult in the first place. One way out of this dilemma is resorting to expert knowledge – 'substantive information on a particular topic, that is not widely known by others' (Martin *et al.*, 2012). Such knowledge may fill an information gap (Keith *et al.*, 2004; Runge *et al.*, 2011), but because experts can easily make mistakes (Tversky & Kahneman, 1974; Ludwig & Mangel, 2001), their knowledge should be subject to testing and

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verification (Burgman *et al.*, 2011). In the context of biological diversity, species rarity is a good example of the sort of information that is frequently provided by experts (e.g. Stotz *et al.*, 1996; IUCN, 2001; Franklin *et al.*, 2009; ACCDC, 2012). Rare species are particularly prone to extinction (Lande, 1988; Lawton, 1995; Stephens & Sutherland, 1999; Saether *et al.*, 2010), and thus, many management decisions require information on which species are common and which species are rare. But rare species are also hard to find by definition, and the accurate quantification of their rarity, however measured, is a challenging and expensive task. As a result, many assessments of rarity constitute highly uncertain compilations of the opinion of a few professionals and are rarely validated against empirical data. This article offers a test of expert knowledge about rarity of tropical forest birds, discussing the usefulness of this knowledge and the reasons why experts may or may not have been correct in our particular case.

There are multiple definitions of rarity (Rabinowitz *et al.*, 1986; Hartley & Kunin, 2003), which can be broadly organized in two groups (Gaston, 1994, chapter 1): those which treat rarity as low population size and those which treat it as small geographic range, or area of occupancy. In this study, we define rarity as low occupancy, *that is* low probability that a site is occupied by a species. Although no definition is perfect, we chose an occupancy-based rather than abundance-based definition because this suits the large spatial extent and the field sampling constraints of our study. Whether one species is rare or not depends on an arbitrarily low number of individuals or number of occupied sites below which we declare rarity; when working with two or more species, however, one species can always be more rare than the other, and rarity becomes a relative concept. We treat rarity in its relative form, and test predictions about which species are rare and which are common in pairwise comparisons of closely related species.

The main danger in classifying species as rare or common is to confound rarity with elusiveness. In the absence of misidentification (Miller *et al.*, 2011), detection is a sure sign of presence, but nondetection can result from real absence or from missing a species that is actually there. A large number of studies show how failure to account for imperfect detection may bias down estimates of occupancy or population size (e.g. Moilanen, 2002; Gu & Swihart, 2004; Kéry & Royle, 2008), sometimes in extreme ways (Simons *et al.*, 2009; Kéry *et al.*, 2010). We address this problem with a well-established occupancy-sampling design (MacKenzie *et al.*, 2002; Tyre *et al.*, 2003) that includes replicate visits to each of a set of sites within a relatively short period. Essentially, replicate visits take place within a short enough time that one can consider the site to be closed (i.e. either occupied or not for the entire set of replicates). The proportion of detections over the total number of visits to sites with one or more detections reveals information about detection probability, which in turn improves inference about the number of sites where the species may be present yet not detected. This leads

to estimates of real occupancy, unbiased by imperfect detection, which we compare to an *a priori* hypothesis of which species are rare and which are common.

Our source of expert knowledge was the ornithological monograph by Cohn-Haft *et al.* (1997) and subsequent consultation with its authors. Based on more than 10 years of opportunistic observations in three large areas of forest and one river margin, the monograph updates a species list for one of the forest areas (Stotz & Bierregaard, 1989) and offers the most complete description of the avifauna around the city of Manaus available to this date. The three authors, M. Cohn-Haft, A. Whittaker and P. Stouffer, are all professional ornithologists who jointly had 25 years of experience in the region when the monograph was published and continue working in the region today. Cohn-Haft *et al.* (1997) offered qualitative ratings of species rarity and commonness-our interest in testing expert knowledge stems directly from their challenge that 'ratings represent dimensionless hypotheses of density that can (and should) be tested by quantitative census techniques'. To test the ratings, we focus on ten pairwise comparisons of closely related species in an effort to separate interspecific occupancy differences from other biological differences that might confer rarity. In each pair, one species is hypothetically common and the other is hypothetically rare. Our null hypothesis is that all rating differences are false: there is no difference in occupancy between species of the same pair, and any impression of such difference is due to sampling artefact.

While Cohn-Haft *et al.* (1997) made pioneering observations of an avifauna that was still poorly identified, we had the opportunity to conduct a designed sample of a target study area and to employ a simple but multifaceted combination of observation techniques that maximizes the detection of focal species. We also trained observers to identify bird vocalizations, tested their ability to identify vocalizations correctly, and modelled species detection as a function of observer performance metrics. We did not model occupancy as a function of habitat covariates, as our purpose was to compare species and not to ask about reasons that may underlie within-species variation in rarity or occupancy. The focus on simple comparisons of occupancy and the flexibility with sampling techniques afforded a relatively large spatial and temporal coverage. We hope that our focused approach, aligned with the breadth and impact of Cohn-Haft *et al.*'s (1997) monograph, offers an informative test of expert knowledge about rarity and commonness of central Amazon birds, and a useful illustration of the assessment of expert knowledge in an ecological setting.

METHODS

Study area

Field sampling took place on the trail grid of 'camp 41' at the Biological Dynamics of Forest Fragments Project (BDFFP), 70 km north of Manaus, Brazil. The grid spans

1000 ha of upland primary tropical moist forest adjacent to km 41 of the ZF-3 road, off the interstate highway BR-174 (Fig. 1a). Forest canopy is 35–40 m tall with emergent trees as high as 45 m; the sparse understorey vegetation, dominated by stemless palms contrasts with a dense tree cover (Rankin-de-Mérona *et al.*, 1992). Annual rainfall ranging from 1900 to 3500 mm falls mostly between January and May, with a dry season from June through December when it usually rains < 200 mm per month (Laurance, 2001). The sampling grid overlaps four microbasins that drain into the Urubu River and contains two ponds, both surrounded narrowly by relatively low forest. Strong winds in September 2007 created two large tree-fall gaps of more than one hectare each. We distributed 55 sampling points at regular 400-m intervals along 10 parallel north–south trails, themselves separated from each other by 400 m, except for the two central trails separated by 600 m on either side of a particularly steep valley (Fig. 1b).

Species and ratings

We selected 10 species pairs, each formed by one hypothetically common and one hypothetically rare species, henceforth called 'common' and 'rare', respectively (Table 1). *A priori* ratings of rarity followed Cohn-Haft *et al.*'s (1997) listing of species under common (c), uncommon (u) and rare (r) cate-

Figure 1 Location of sampling grid within study area in northern South America. Top panel (a) shows the BDFFP east of highway BR-174 with unpaved roads (dashed line) and streams (grey lines); dark grey is primary forest and light grey is pasture or second growth. The sampling grid for this study (b) spans an area of 928 ha near km 41 of the ZF-3 road; it includes 55 sampling points connected by trails accessible from 'camp 41'.

gories. Given the broad qualitative nature of the categories and our relative approach to rarity, we formed pairs of common and rare species that had ratings of (c,r), (c,u) and (u, r). In two of the pairs (foliage-gleaners and antthrushes), the published ratings were (c,c), but we revised them upon consultation with the experts: the rare foliage-gleaner is considered common in secondary forests but rare in the old-growth habitat that dominates the region; the rating of the antthrushes was revised based on post-1997 observations suggesting that *Formicarius analis* is rarer than *F. colma*. Eight of 10 pairs were formed by congeneric species; the remaining two consisted of ecologically and morphologically similar species from the same family. Relatedness was intended to reduce phylogenetic variability within each pair, enabling us to isolate and explore differences in rarity on a common evolutionary background. All species are resident throughout the year and have vocalizations that are relatively easy to identify. In an attempt to attain independence between points, we avoided species with very large territories and/or loud calls, such as tinamous, hawks, toucans, parrots, macaws and cotingas.

Field sampling

We sampled during three field 'seasons' in December 2007, May 2008 and November 2008. We call these D-07, R-08 and D-08 because they fall respectively in dry, rainy and dry periods. Seasons lasted 11, 13 and 12 days, respectively, during which we sampled each of the 55 points from a minimum of nine replicate visits in D-07, to a maximum of 27 in D-08. Intervals between visits were such that we assume closure within, but not between seasons. Data collection followed three techniques: point counts, playback and autonomous recording. D-08 received more visits because we started employing autonomous recording then and recorders make it easier to replicate visits. Sampling started 10 min before sunrise and went on for up to 4 h. We always registered the time at which we visited each point and used that information as a covariate of detection probability in the analysis. A point count consisted of a 3-min visit to a sampling point where an observer registered the names of all species seen or heard. To cover the whole grid shortly, we performed simultaneous point counts with ten observers for seven consecutive days in each season. Each day observers were randomly assigned to the 10 north–south trails (Fig. 1b), starting at the southern end of each trail, moving north, and then returning southbound on an adjacent trail. Playback sampling was conducted at the same points for up to five consecutive days, always at the end of each season after all point counts were performed. One observer (MCC) broadcast vocalizations of focal species to elicit behavioural responses (vocalization or approach) that would permit detection of the species' presence at a point. We only applied playback to trogons, puffbirds, woodcreepers, antshrikes, antthrushes and wrens – groups that, in our experience, respond particularly well to this technique. Playback sampling took
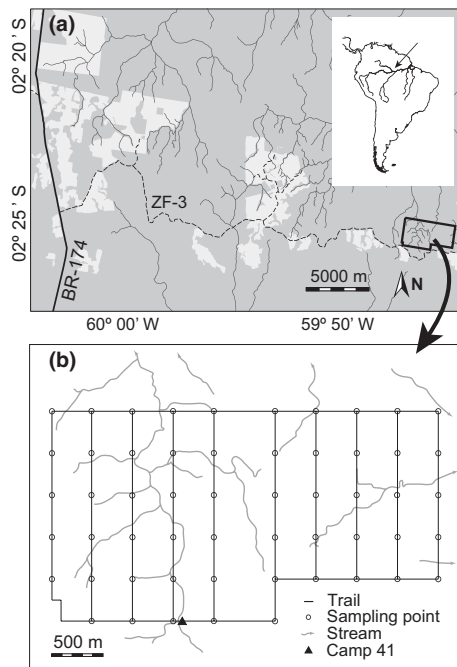
Table 1 Species pairs, with number of sampling seasons per pair and model selection results

Pair	Species*	k†	Model‡	w_i§
Trogons	*Trogon viridis* *Trogon rufus*	3	$\psi\,(t \times s)\,,\,p\,(t + s + h \times s + r + \text{Pb} \times s + \text{Sc} + R)$	0.500
Puffbirds	*Bucco tamatia* *Bucco capensis*	2	$\psi\,(t + s)\,,\,p\,(t + h + \text{Pb})$	0.197
Jacamars	*Galbula dea* *Galbula leucogastra*	2	$\psi\,(t \times s)\,,\,p\,(t + h + r + \text{Sc} + R)$	0.313
Woodcreepers	*Dendrocolaptes certhia* *Dendrocolaptes picumnus*	3	$\psi\,(t + s)\,,\,p\,(t + s + h \times s + r + \text{Pb} \times s + \text{Sc} + R)$	0.508
Foliage-gleaners	*Automolus infuscatus* *Automolus ochrolaemus*	2	$\psi\,(t + s)\,,\,p\,(t + s + h \times s)$	0.424
Antshrikes	*Cymbilaimus lineatus* *Frederickena viridis*	2	$\psi\,(t + s)\,,\,p\,(t + s + h + \text{Pb})$	0.288
Antwrens	*Myrmotherula brachyura* *Myrmotherula axillaris*	3	$\psi\,(t + s)\,,\,p\,(t + s + h + \text{Sc} + R)$	0.292
Antthrushes	*Formicarius colma* *Formicarius analis*	3	$\psi\,(t + s)\,,\,p\,(t + s + h + \text{Pb} + \text{Sc} + R)$	0.471
Wrens	*Microcerculus bambla* *Cyphorhinus arada*	2	$\psi\,(t + s)\,,\,p\,(t + s + h + \text{Pb})$	0.217
Greenlets	*Hylophilus muscicapinus* *Hylophilus thoracicus*	2	$\psi\,(t + s)\,,\,p\,(t + s + h + \text{Sc} + R)$	0.286

*The first species of each pair is hypothetically common and the second is hypothetically rare.

†Number of sampling seasons. When $k = 2$ the rainy season of 2008 was dropped due to lack of data.

‡The top model (ΔAIC = 0) for the respective species pair with model name listing covariates for occupancy (ψ) and detection (p) in parentheses. Covariate notation stands for sampling season (t), species (s), time (h), previous-night rain showers (r), playback (Pb), observer score (Sc) and autonomous recording (R). Simple additive effects are denoted by '+'; '×s' indicates an interaction between the covariate before the '×' and species.

§AIC weight of the top model within the *a priori* set of 22 models.

27 minutes per point: starting with 3 min of silence, followed by 1 min of playback and 2 min of listening per species. Instead of playing songs of all twelve playback species on every point, we randomly selected four pairs per point and played the voices of selected species in a random sequence.

When sampling with autonomous recorders, we placed portable autonomous recording devices (PARD) at selected points to record nonstop and unassisted for 40 h, or two consecutive mornings. PARDs were assembled at the BDFFP by CN and MCC following a design by Kurt Fristrup; each device consisted of an mp3 recorder, two surveillance microphones with built-in amplification, a power supply and a waterproof case. Microphones were mounted in the neck of a laboratory funnel, which provided protection and additional amplification (Fristrup & Clark, 2009). Ten PARDs were set on the sampling points of two adjacent north–south trails and subsequently moved to the next set of two trails, until covering the whole grid. Each morning's recording was split into five 5-min cuts taken 15 min prior to sunrise and 15, 45, 75 and 105 min after. Cuts were processed in the laboratory by MCC, producing records of detection and nondetection of all focal species in each cut.

Because different observers have different abilities to hear and identify bird vocalizations, point counts by ten different people result in heterogeneous data quality. We addressed this problem with a computer-based system for assisting in memorizing bird sounds based on SUPERMEMO, a spaced-repetition software (Wozniak, 2006; Ferraz *et al.*, 2008; Greene, 2008). The system helped to balance skills across observers and produced a quantitative score of observer ability. Our *SuperMemo* study collection includes 863 mp3 tracks of 337 species, based on field recordings kindly shared by Philip C. Stouffer and the Ornithological Collection of the *Instituto Nacional de Pesquisas da Amazônia* (INPA). *SuperMemo* presents bird vocalizations to the user in the form of questions, which he answers with a species name, as if using a collection of electronic flash cards. The system tracks user performance and runs an algorithm that adjusts the timing of future questions to enhance memorization of the most frequently missed sounds. At the beginning of each season, we used *SuperMemo* to obtain a memorization score for each observer. The score measures the proportion of focal species' vocalizations that the observer identifies correctly in a test and was included as a covariate of detection probability in occupancy models.

Analysis

We used point count, playback and recording data jointly, to estimate site occupancy by each species. Operationally, a 'site' is an area with a radius of 200 m centred on a

sampling point. We believe this radius is the maximum distance at which an observer or a recorder can pick up a sound from the loudest of our study species. Site occupancy estimation formally accounted for imperfect detection following the standard maximum likelihood hierarchical approach introduced by MacKenzie *et al.* (2002) and expanded by MacKenzie *et al.* (2005). Just as in the standard approach, our models contain a sampling level describing the probability of detection conditioned on occupancy (p), and an underlying biological level describing the probability ψ that a site is occupied. Both p and ψ are allowed to vary between seasons, yet for simplicity and ease of numerical estimation, we model temporal dynamics implicitly (MacKenzie *et al.*, 2006, p. 186), without quantifying the dynamic processes of local extinction and colonization, which are not central to our goals. Also adhering to standard, we incorporate the flexibility of linear models by representing both p and ψ as logistic functions of sampling, environmental and temporal covariates. The one nonstandard aspect of our analysis is the testing of rarity hypotheses by modelling one pair of species, rather than one single species, at a time. In doing so, we treat species identity as a binary covariate estimating the 'effect' (α_1) of species identity on ψ, while also considering the possibility of a species 'effect' (a_1) on p. Note that the same covariate, species (s), can have different effects on occupancy and on detection. A simple model for one pair would be:

$$\begin{cases} \text{logit}(p_i) = a_0 + a_1 s_i \\ \text{logit}(\psi_i) = \alpha_0 + \alpha_1 s_i \end{cases},$$

where 's' equals 0 for the common species ($i = 1$) and 1 for the rare ($i = 2$). One can then add effects a_2, a_3, … or α_2, α_3, … for additional covariates of detection or occupancy, respectively. There are several informative ways of combining species ($i = 1, 2$), season ($j = 1, 2, 3$) and visit ($k = 1, …, 27$) attributes as covariates in a model; we fit the same set of 22 models defined *a priori* to each pair of species, each model representing an alternative hypothetical explanation of the data. Every model includes α_1, but some exclude a_1 to examine whether species differences can be due to occupancy alone.

Our model set is based on a core group of four alternative detection model types (Table 2). These range from a *Simple* to a fully parameterized (*Full*) arrangement of biological and sampling technique covariates. Biological covariates are the time of day (h) and a binary measure of whether there was heavy (>10 mm) rainfall the night before sampling. Technique covariates are: a binary measure of playback (Pb; equal to 1 when there is playback and 0 otherwise), a quantitative score of observer ability (Sc), and a binary measure of PARD use (R; equal to 1 for PARD samples and 0 otherwise). Additionally, we model interactions between h and species ($h \times s$) as well as between Pb and species (Pb $\times s$), allowing for species-specific detection responses to time of day and playback. Intermediate model types differ from the *Simple* type by the inclusion of interactions (*Intermediate 1*) and by

Table 2 Basic structure of detection models indicating four alternative arrangements of the linear effects of time (h), playback (Pb), observer score (Sc), autonomous recording (R) and previous-night rain showers (r) on logit detection probability; '$\times$' indicates an interaction between the covariate before the '$\times$' and species (s). The 22 models that were fitted to each species pair's data are combinations of these four basic types with different effects of sampling season and species on occupancy and detection

Model type	Detection model covariates						
	h	h $\times$ s	r	Pb	Pb $\times$ s	Sc	R
Simple	$\times$			$\times$			
Intermediate 1	$\times$	$\times$		$\times$	$\times$		
Intermediate 2	$\times$			$\times$		$\times$	$\times$
Full	$\times$	$\times$	$\times$	$\times$	$\times$	$\times$	$\times$

the inclusion of Sc and R (*Intermediate 2*). We combine the four basic types with three ways of modelling seasonal (t) and species (s) effects on detection: additive ($t + s$), interaction ($t \times s$) and season alone (t), this latter hypothesizing equal detection between species. As *Intermediate 1* does not apply in the absence of a species effect, the combination originates eleven detection models. The occupancy part of the model is focused on seasonal and species effects, taking only two alternative forms: $t + s$ and $t \times s$. The combination of eleven scenarios for detection and two for occupancy leads to the 22 models of our *a priori* set. The most parameterized model is the full-detection model with three seasons and interaction between species and season both on occupancy and detection:

$$\begin{cases} \begin{aligned} \text{logit}(p_{ijk}) = & a_0 + a_1 s_i + a_2 t'_j + a_3 t''_j + a_4 s_i \times t'_j + a_5 s_i \times t''_j \\ & + a_6 h_k + a_7 s_i \times h_k + a_8 r_k + a_9 \text{Pb}_k + a_{10} s_i \times \text{Pb}_k \\ & + a_{11} \text{Sc}_k + a_{12} R_k \end{aligned} \\ \text{logit}(\psi_{ij}) = \alpha_0 + \alpha_1 s_i + \alpha_2 t'_j + \alpha_3 t''_j + \alpha_4 s_i \times t'_j + \alpha_5 s_i \times t''_j. \end{cases}$$

Covariate t'_j equals 1 for D-07, -1 for R-08 and 0 for D-08, while t''_j equals 1, 0 and -1, for D-07, R-08 and D-08, respectively. With this parameterization of seasonal effects, a_1 and α_1 can be interpreted as average effects of species across seasons, regardless of whether there are any interactions in the detection or occupancy part of the model. All the other models are simplifications of this one.

Data analysis included model selection and parameter estimation, both implemented in the freely available software PRESENCE (Hines, 2012). We chose how to model each pair's data based on model selection results (Table 1), but tested the null hypothesis of equal occupancy within pairs by examining α_1 estimates. Model selection followed the Akaike information criterion (AIC), which formally expresses a compromise between model fit and parsimony (Burnham & Anderson, 2004). Worse fit or higher number of parameters result in higher AIC values. We rank models based on two

AIC-related metrics: ΔAIC, the difference between a model's AIC and the lowest AIC value in the model set; and AIC weight (w_i), interpreted as the contribution of a given model to explaining the data, relative to other models. The sum of w_i's across the model set equals 1. The null hypothesis predicts that α_1 should be equal to or very close to zero. Thus, the signal of α_1 estimates from a set of species pairs should be positive or negative with equal probability (0.5), as in a coin toss.

RESULTS

The minimum number of samples per point was nine in D-07 and eleven both in R-08 and D-08. Jointly, the three seasons had at least 37 visits per point. The most frequently detected species was the buff-cheeked greenlet *Hylophilus muscicapinus* (all Latin names based on Remsen *et al.*, 2012), with 260 detections, and the least was the buff-throated foliage-gleaner *Automolus ochrolaemus*, only heard or seen eight times throughout the study. Lack of observations led us to remove the only rainy period, R-08, from the analysis of six species pairs (Table 1). Although we present results for all ten pairs, lack of data on *A. ochrolaemus* precluded occupancy estimation for that species (Fig. 2) and, consequently, there is no occupancy slope parameter for foliage-gleaners (Fig. 3).

We were able to fit all 22 models to all species pairs, and all pairs had top-ranking models (ΔAIC = 0) with an AIC weight (w_i) higher than 0.19 (Table 1). Overall, additive models of the effect of season and species on occupancy ranked better than interaction models, which allow for change in species effects across seasons. Interaction occupancy models only ranked at the top for trogons and jacamars, both with extremely high occupancy estimates for the common species in R-08. Temporal variation of trogon occupancy warns against any strong statement about which species is most common; for jacamars, however, the interaction between species and season does not obscure the consistently higher occupancy for paradise jacamar *Galbula dea* than for bronzy jacamar *Galbula leucogastra* (Fig. 2).

Differences within pairs of species are best summarized by the slope parameters that measure species effects on occupancy (α_1, Fig. 3a) and detection (a_1, Fig. 3b, Table 3). We found no evidence of within-pair differences for puffbird and jacamar detections, which had top models without any effect of species on detection. There were measurable differences, however, for all remaining pairs: three of them (trogons, antthrushes, and wrens) showing higher detection probability for the rare species (positive a_1) and five for the common (negative a_1). Of the nine α_1 estimates, eight were negative, that is, revealed lower occupancy for the rare than for the common species, in agreement with expert knowledge. Only antwrens defied expectations, with slightly higher occupancy for the white-flanked antwren *Myrmotherula axillaris* than for the pygmy antwren *Myrmotherula brachyura*. Nonetheless, it is highly improbable that the results would arise from chance under a true null hypothesis: if the sign of α_1 followed a binomial distribution with probability of success 0.5, the overall result of eight successes in nine trials would have a probability of approximately 0.017. The probability of an equal or more extreme result (eight or nine successes) would be lower than 0.02.

Detection probabilities were generally low but variable across species and time (Fig. 4). One-half of the pairs that had three seasons of data had minimum detection probabilities in R-08. Every time we had to exclude one season for lack of detections, the excluded season was R-08. Although detection showed a strong association with season, and apparently with seasonal rain, it showed no overwhelming relation to shorter-term overnight rain showers. Table 3
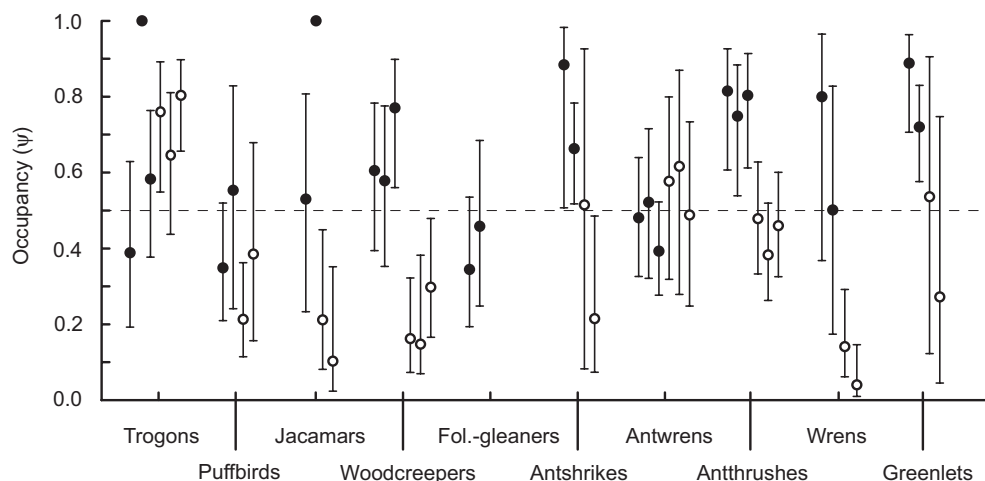

Figure 2 Occupancy estimates with 95% confidence intervals for the ten species pairs, excluding *Automolus ochrolaemus* (Buff-throated Foliage-gleaner). Filled and empty circles show common and rare species, respectively, with one estimate per sampling season. Variances could not be obtained for the two occupancy values shown without confidence intervals.
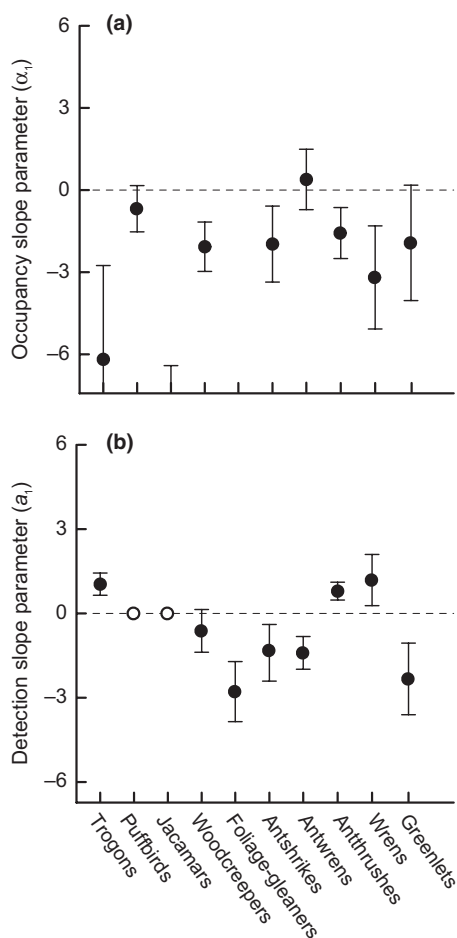
Figure 3 Difference in occupancy (a) and detection (b) between hypothetically common and rare species. 'Slope parameters' on the *y*-axis refer to an imaginary line joining estimates of occupancy (or detection) for the two species in each pair: a positive slope means the rare species has the highest occupancy (or detection); a negative slope indicates the opposite relationship. The occupancy slope for jacamars is negative beyond the *y*-axis display range, and the occupancy slope for foliage-gleaners could not be estimated because there were no estimates of occupancy for one of the species in the pair. The top model for puffbirds and jacamars had no effect of species on detection probability, hence the empty circles on panel b.

shows only three top models with an effect of overnight rain (r) on detection but only one (trogons) where the effect differs from zero beyond the 95% confidence level. Time of day (h) was the most broadly relevant covariate of detection; its effect was significantly different from zero in eight of ten cases and negative in all but one. With the exception of jacamars, all pairs were more easily detected early rather than late in the morning. There was a strong positive interaction between time and species (s) for trogons and foliage-gleaners, indicating that, for these pairs, the negative effect of time is due to the common species. Playback (Pb) had a positive effect on detection every time that it was used; the effect was significantly different from zero in all but one of its

estimates. The strongly positive interaction between playback and woodcreeper species reveals a much stronger response to playback from the black-banded woodcreeper *Dendrocolaptes picumnus* than from the barred woodcreeper *Dendrocolaptes certhia*. As with playback, the effect of the observer ability (Sc) was positive every time it was estimated; in four of six cases, its 95% confidence interval excluded zero. Detection with autonomous recorders (R) was significantly higher than detection with point counts for two species pairs (Woodcreepers and Antthrushes) but significantly lower in two others (Trogons and Antwrens; Table 3, last column).

DISCUSSION

We reject the null hypothesis of no difference in occupancy between species of the same pair. Had expert knowledge been wrong, estimates of α_1 should have been positive just about as often as negative. Instead, α_1 was negative in eight of nine cases, indicating that the hypothetically rare species indeed occupy fewer sites than the hypothetically common ones, and confirming that *a priori* expert ratings were broadly correct. Our observations thus match predictions about who is rare and who is common and we conclude that expert knowledge can be useful and is worthwhile eliciting.

Could we find this match by chance? One might argue that by looking at a relatively small area over a short period of time, we stumbled across a scenario that matches expert predictions yet is not sufficiently relevant to the region where predictions apply. Clearly, the spatial scope of our sample was smaller than the spatial scope of predictions in Cohn-Haft *et al.* (1997), so there may be interesting spatial variability in occupancy that is not captured in our analysis. Nonetheless, our sample spanned an area one order of magnitude larger than classical tropical bird surveys (Karr, 1990; Terborgh *et al.*, 1990; Thiollay, 1994) and focused on a site that contributed substantial information to expert predictions. We also find remarkably little evidence of variability in occupancy through time: on the one hand, our estimates support a categorization conceived more than 10 years before our fieldwork, and on the other, we found almost no support for season-species interaction in occupancy, suggesting that within-pair differences have kept the same sign throughout the 12-month span of our fieldwork.

Our confidence that the observed match says something useful about expert knowledge is further supported by the natural history of the only mismatching pair of species: the antwrens. In this pair, the hypothetically rare *M. axillaris* turned out to be the most common species of the pair. Although we cannot rule out the possibility of a true mismatch, we believe the observer's ability to recognize vocalizations offers a plausible explanation for this result. While *M. axillaris* frequently joins understorey mixed-species flocks, where it can be identified by sight and a variety of conspicuous sounds, *M. brachyura* is a canopy species hardly ever seen and easily detected only by its song (Cohn-Haft *et al.*, 1997). Unlike the song, calls of *M. brachyura* are soft and

Table 3 Estimated linear effects of covariates on detection probability; covariate names follow notation in Table 1 and the parameter values correspond to the top-ranking model of each pair.

Pair	Detection covariates and associated parameter estimates							
	s	h	h × s*	r	Pb	Pb × s	Sc	R
Trogons	1.042[†]	−1.229	1.481	−0.602	2.077	−0.428	0.112	−0.897
Puffbirds	–	−0.886	–	–	4.693	–	–	–
Jacamars	–	0.256	–	−0.670	‡		0.599	−0.311
Woodcreepers	−0.621	−0.946	−0.291	−0.248	2.487	3.324	0.110	0.646
Foliage-gleaners	−2.782	−1.513	1.686	–			–	–
Antshrikes	−1.401	−0.240	–	–	1.809	–	–	–
Antwrens	−1.404	−0.146	–	–			0.259	−0.616
Antthrushes	0.794	−0.369	–	–	1.164	–	0.200	0.531
Wrens	1.188	−0.014	–	–	0.882	–	–	–
Greenlets	−2.330	−0.303	–	–			0.246	−0.458

*When the interaction parameter estimate is positive, the respective effect is stronger for the hypothetically rare than for the hypothetically common species; the opposite applies to negative estimates.

†Boldface numbers indicate estimates that are significantly different from zero at the 95% confidence level.

‡Pairs with crossed-out playback parameters had no playback during data collection and no playback effects in any of the models.
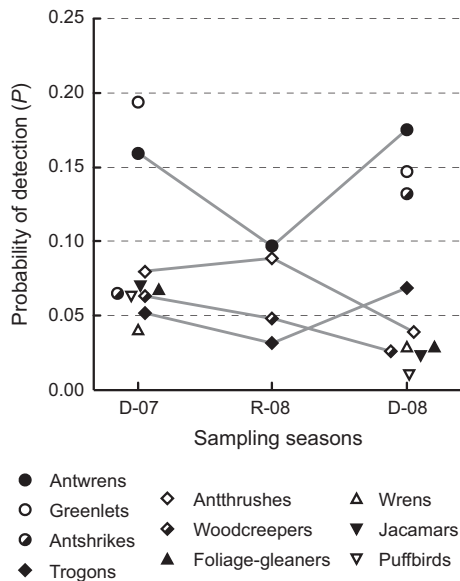

Figure 4 Point estimates of detection probability across seasons. Symbols show a reference estimate of detection for the common species of each pair, at the average sampling time and average observer score, without playback, no autonomous recording and no overnight rain.

that improved detection might result in nine of nine matches.

The quantification of detection probability is central to our approach, both for understanding what animals do and for improving our efforts to find them. From the first perspective, while most pairs in our study confirm the intuition that relatively rare species should be hard to detect, we find three exceptions in trogons, antthrushes and wrens, where it is the lower occupancy species that is easier to detect. Also as expected, detection is higher earlier rather than late in the morning, but again, there is an exception with late-calling jacamars. Rain makes a difference when it pours, but we found little evidence (excepting trogons) that overnight rain affects detection the next morning. As for what we can do to find birds, it is very clear that playback makes a difference: there were strong positive effects on all but one of the tested pairs. Practice also helps detection, particularly with jacamars, antwrens, greenlets and antthrushes, for which observers with a higher score had significantly higher detection. Finally, comparing one three-minute point count with one five-minute autonomous recording sample, we find that relative performance of the two techniques depends on the pair: detection with recorders is clearly better in two cases (woodcreepers and antthrushes) and clearly worse in another two (trogons and antwrens). The decision of whether to use autonomous recorders, however, should also account for the reduced cost of taking replicate samples of a site once the initial investment of buying the recorders is performed. One observer can take at most five samples at peak-calling time in one morning; the same person, however, will take one afternoon to set up five recorders that can each collect as many samples as desired for as many days as battery power allows. Because humans have eyes, they can easily beat recorders in open environments (Hutto & Stutzman, 2009); nonetheless, in closed forests where most work is performed

easily overlooked; these particular calls were not tested in our training (for lack of good study recordings) and may have been missed by most observers. If singing is limited to breeding periods, we could be comparing site occupancy by breeding *M. brachyura* with site occupancy by any individual of *M. axillaris*. This unavailability of nonbreeding *M. brachyura* for detection would bias its occupancy estimate down. Thus, although statistical results would not change much due to an additional matching pair, natural history suggests

by ear, the recorders will save time and supply a permanent archive of observations.

Perhaps, the most defining aspect of our test of rarity predictions is that, to extend the spatial and temporal scope of the study, we treat rarity in terms of number of occupied sites instead of the more direct population metric of number of individuals. This compromise is as useful as the biological information conveyed by the occupancy estimates. While occupancy is an attribute of a site, its precise biological interpretation depends on how individual organisms move through space. When sites are close together and organisms move between them, it is appropriate to interpret occupancy as habitat use (MacKenzie, 2006). A multiscale approach can add a 'use' parameter that quantifies the probability that organisms are available for detection in an occupied site (Nichols *et al.*, 2008; Mordecai *et al.*, 2011); yet, multiscale designs entail adjustments that ideally differ between species. In its simplicity and generality, the two-tiered model that we used is particularly useful for species comparisons, even when variable and unknown movements of organisms heed caution in biological interpretation. Conceivably, one might account for the implications of individual movement by shifting the focus to number of individuals. Yet, the estimation of population size (let alone individual movement rates) presents more difficult sampling and analytical obstacles than the estimation of occupancy, especially in closed forest habitats where low visibility limits the applicability of distance sampling (Simons *et al.*, 2009). So, we do encourage others to make the same compromise that we made for comparing species rarity (or species distributions) when detection is imperfect, and individual-based data are not forthcoming. The approach of inferring site occupancy probability from replicated sampling of multiple sites is valid for a wide variety of species and spatial scales well beyond the scope of this study (McClintock *et al.*, 2010; Gibson, 2011; Katsanevakis *et al.*, 2012; Noon *et al.*, 2012).

Besides the modelling and sampling advantages, the adoption of occupancy in the assessment of rarity finds support in two general relationships that are firmly grounded in the ecological literature: the relationship between occupancy and local abundance, and the relationship between local abundance and species detection probability. The positive relationship between occupancy and local abundance is an extremely recurrent pattern (Gaston *et al.*, 2000) supported by a vast empirical literature (Borregaard & Rahbek, 2010). If locally abundant species also have large ranges, then we expect occupancy-based and abundance-based metrics to offer similar views of who is rare and who is common, which justifies taking the most practical approach of sampling sites instead of individuals. When sampling sites, detection of the species requires detection of at least one individual of the species, and herein lies the connection with the second relationship – that probability of detecting a species is positively associated with the local number of individuals (Royle & Nichols, 2003). If both relationships are true, it follows that (1) common (high occupancy) species should be relatively easy to detect wherever they occur and (2) expert predictions of rarity should not fail too frequently on the basis of detection failure. While these conclusions do not undermine the importance of accounting for detection errors, we believe they reinforce the value of expert knowledge on species rarity and partially explain the results of this study.

Given the weight that notions of rarity carry in population biology and wildlife management, it is essential that we quantify them with an appropriate assessment of uncertainty (IUCN, 2011). When working with field observations, such assessments should formally account for the imperfections of the sampling process, whether the goal is to measure the extent of a distribution or to examine relations between environmental factors and the probability of species occurrence (Kéry, 2011). When field data are unavailable or insufficient, however, much can be performed before accepting inaction on the grounds of insufficient knowledge. While expert knowledge contains an element of subjective judgement that may increase bias and uncertainty in quantitative assessments (McCarthy *et al.*, 2004), our results show how experts can make useful predictions about species rarity and commonness. This should be motivation for taking expert knowledge seriously and for eliciting it in ways that maximize its usefulness. There is a growing literature on how to systematically elicit expert knowledge (Kuhnert *et al.*, 2010; Martin *et al.*, 2012), as well as examples of how it can help guide conservation decisions (Keith *et al.*, 2004; Martin *et al.*, 2011). Some elicitation tools are specifically designed for quantifying probabilities of success (e.g. a probability that a species is present at a site) using the same logit-linear model structure that we used in this study (Low-Choy *et al.*, 2009a). Rigorous and creative eliciting methods may thus provide information that can be a guide to action on its own right, a basis for empirical testing of expert predictions, or a source of prior information in Bayesian updating (Low-Choy *et al.*, 2009b). We hope this study fosters a productive combination of elicitation and empirical tests that will help cover information gaps and stimulate empirical research.

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