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Transience in the humpback whale population of New Caledonia and implications for abundance estimation

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Abstract

A phenomenon of transience in the humpback whale population breeding in New Caledonia has been highlighted in recent analyses. We used these data to illustrate the risk of flawed inference when transience is not properly accounted for in abundance estimation of resident populations. Transients are commonly defined as individuals that pass through the sampling area once, *i.e.*, have a null probability of being caught again, and therefore induce heterogeneity in the detection process. The presence of transients can lead to severe bias in the estimation of abundance and we demonstrate how to correct for this feature when estimating abundance of resident populations. In New Caledonia, very different conclusions about the number of resident whales in the southern lagoon between 1999 and 2005 are obtained when the abundance estimate accounts for the transient whales. Without correction, the estimates of the abundance were up to twice as high across all years compared to the estimates of the resident population when a correction for transients had been incorporated. Having reliable population estimates when assessing the status of endangered species is essential in documenting recovery and monitoring of population trends. Therefore, we encourage researchers to account for transients when reporting abundances of resident populations.

Key words: modeling transients, abundance, bias, population size estimation, humpback whale, two-age-class model, Cormack-Jolly-Seber model.

Humpback whales that congregate to breed during austral winter in the South Pacific have been studied since the 1990s. These studies used photo-identification analysis strengthened by genotype comparisons to highlight fidelity to local wintering grounds and a low level of migratory exchange among wintering grounds (Garrigue *et al.* 2002, 2011; Olavarría *et al.* 2007). Although site specific fidelity was detected, population-specific analyses suggested a phenomenon of transience, or whales just passing through the study area once, in the population breeding in New Caledonia (Constantine *et al.* 2012, Madon 2010).

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Estimates of population abundance serve to determine population trends essential to evaluate viability of IUCN endangered populations (Childherhouse *et al.* 2008). The reliability of these estimates depends upon the underlying assumptions of the models used. In particular, the assumption of equal probability of capture is likely to be violated with migratory animals such as humpback whales if immigration or emigration occurs. Transience is a case of emigration and implies a null recapture probability (Pradel *et al.* 1997). This leads to heterogeneity in the detection process, which, in turn, can induce severe bias in the estimation of abundance (*e.g.*, Cubaynes *et al.* 2010). Some studies on cetaceans have considered the effects of transience (Ramp *et al.* 2006, 2010; Silva *et al.* 2009) but only one attempted to correct for it while estimating population size (Conn *et al.* 2011). Here, we illustrate the risk of flawed inference when transience is not properly accounted for and demonstrate how to incorporate a correction for the transient effect when estimating abundance of the resident populations.

Materials and Methods

Sampling Protocol and Data Sets

In New Caledonia mark-recapture data were mainly collected in the southern lagoon between 1999 and 2005 on a daily basis between July and September, weather conditions permitting. The sampling area randomly surveyed covered approximately 621 km. When a whale or a group of whales was encountered, an attempt was made to obtain a photograph for photo-identification and a skin sample for genotyping from each of the individuals present in the group. Photographs and genotypes were reviewed for quality control (QC). Photographs were evaluated under a protocol developed to rank their quality (Calambokidis *et al.* 2001). Genotype samples with fewer than nine microsatellite loci were deleted from the data set (Garrigue *et al.* 2004).

Statistical Analyses

Over the 7 yr of the survey, assuming a closed population was unrealistic, therefore we used the Cormack-Jolly-Seber (CJS) open-population model with time-specific detection probabilities and constant survival to estimate yearly abundances N_t (Williams *et al.* 2002). Standard errors for N_t were estimated using the delta method. When evaluating the fit of the CJS model to the data using goodness-of-fit tests, we found a lack of fit mostly explained by a chance of recapture of first-encountered individuals which was lower than that of previously-encountered individuals. This was specifically tested using a contingency table test (test 3.SR two-sided signed square root [Z] of the Pearson chi–square statistic; Pradel *et al.* 2005) implemented in program U-CARE (Choquet *et al.* 2009). While test 3.SR was not significant on the photographic data set ($Z = 1.42$, $P = 0.15$), the genetic data set revealed the presence of transients in the population of the southern lagoon when males and females were analyzed jointly ($Z = 3.07$, $P < 0.01$). When test 3.SR was run on each group, the result was significant for males ($Z = 2.57$, $P = 0.01$) and females when a one-sided test was performed ($Z = 1.73$, one-sided $P = 0.04$). Consequently we decided to estimate the proportion of transient individuals in the samples. To do so, we followed

Pradel *et al.* (1997) and fitted a model with two age-classes on the survival probability, where age in a mark-recapture context is the time elapsed since first capture. Transients are therefore included in the first age class, the survival of which is the product of the survival of the second age class by the proportion of residents among the unmarked. As a result, the transient proportion among the unmarked τ can be estimated as:

$$\tau_{.} = 1 - \frac{\phi^{*}_{.}}{\phi_{.}} \tag{1}$$

Where $\phi^{*}_{.}$ is the apparent survival rate of individuals newly captured and $\phi_{.}$ the survival rate of residents obtained from the individuals captured more than twice (Pradel *et al.* 1997). We used program MARK (White and Burnham 1999) to fit two age-class models on the photographic and genetic data sets. We tested time and sex effects on the detection and survival probabilities, keeping the two-age structure on survival. Based on AICc (Burnham and Anderson 2004), a model with constant survival and time-dependent detection and a model with survival and detection constant over time were best supported by respectively the photographic and genetic data, although a sex effect was detected on the detection probability with genetic data (Appendix S1). Assuming that residents and transients have similar initial capture probabilities, the proportion of transients T_t in the whole population (marked and unmarked) is the proportion of unmarked individuals at occasion t multiplied by the proportion of transients among the unmarked sample:

$$T_t = \frac{E(u_t)}{E(u_t + m_t)}\tau_{.} \tag{2}$$

where $E(u_t)$ is the expectation of the number of unmarked individuals captured for the first time at occasion t and $E(u_t + m_t)$ the expectation of the number of individuals captured at occasion t (marked m_t + unmarked u_t). We used the observed u_t and $u_t + m_t$ as estimates for $E(u_t)$ and $E(u_t + m_t)$, respectively (Perret *et al.* 2003). A transience-corrected estimator of the number of residents $\hat{N}^{*}_{t}$ was obtained as

$$\hat{N}_{2at}(1 - T_t) \tag{3}$$

Where $\hat{N}_{2at}$ is the abundance estimator at occasion t calculated as $\frac{n_t}{p^*}$ where n_t is the total number of individuals captured at time t and p^* is the detection probability estimated with the 2-age-class models (Appendix S1). We used a nonparametric procedure to obtain the standard errors for $\hat{N}^{*}_{t}$ (Appendix S2).

RESULTS

Sampling effort and data set are summarized in Table 1. The photographic data set analyzed here contained a total of 171 capture histories, whereas the genetic data set comprised 140 capture histories for males and 101 for females (Table 1). Sex data only refers to the genetic data set.

Table 1. Sampling effort and data collected in the southern lagoon in New Caledonia between 1999 and 2005.

Year	1999	2000	2001	2002	2003	2004	2005
Number of days at sea	46	50	55	35	40	11	35
Time at sea	267 h 23 min	311 h 50 min	388 h 33 min	220 h 20 min	266 h 51 min	73 h 50 min	245 h 36 min
Number of nautical miles	2,581	2,661	3,717	2,109	2,316	567	2,492
Number of whales photographed	17	33	51	18	43	17	41
Yearly photo resights		3	9	8	14	4	13
Number of whales genotyped	24	42	66	27	59	21	54
Year-to-year resights		3	8	7	14	5	15

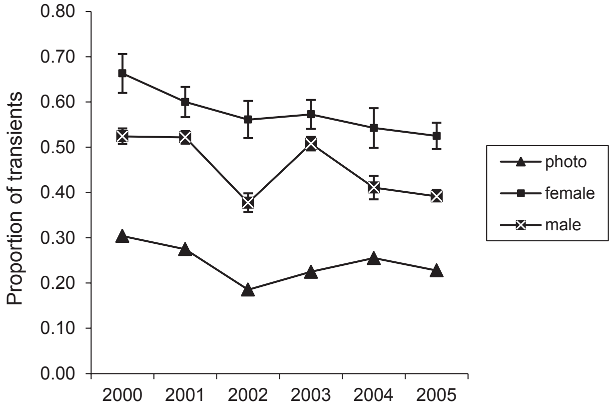

Figure 1. Proportions of transients in the whole population from the photographic data set and of male and female transients in the genetic data set between 2000 and 2005.

The phenomenon of transience revealed by the goodness-of-fit tests in the humpback whale population of the southern lagoon of New Caledonia appears nonnegligible (Fig. 1).

Photographic Data Set

Although transience was statistically detected only in the genetic data set, the average of transients in the whole population (*i.e., T*) for the photographic data set was 25% with the smallest estimate of transients of 19% in 2002 and a peak of 30% in 2000. Given this nonnegligible proportion of transients present in the photo-identification data set, we applied the correction: the corrected estimates of population size were between 18% and 30% smaller than the uncorrected estimates, *e.g.,* in 2000, 95 (CI = 55, 161) for the corrected estimate *vs*. 136 (CI = 71, 259) for the uncorrected one (Table 2).

Genetic Data Set

The proportion of transients in the genetic data set was higher than in the photo-identification data set with an average of 58% for females and 44% for males. These proportions were at a minimum in 2005 with 52% for females and 39% for males (Fig. 1) and were the largest in 2000 with 66% for females and 52% for males. All standard errors for the proportion of transience were smaller than 0.05.

The proportion of transient females was systematically larger than the proportion of transient males (*e.g.,* in 2001 60% of the females were transients *vs*. 51% of males, Fig. 1). This difference was significant in all years ($Z > 2.6$, $P < 0.05$ for a two-sided test).

Ignoring the presence of transients and using those uncorrected estimates for the southern lagoon population led to a serious overestimation for the resident population: *e.g.,* in 2001 the uncorrected estimate by genetic methods suggested a population of males of 188 (95% confidence interval CI = 136, 259), while correcting for transience indicated a resident population of 92 (CI = 44, 195) (Table 2).

DISCUSSION

The presence of transients in a population has several important implications, and quantifying transience has the potential to improve our understanding of other aspects of biology, such as behavior and population structure. Our results confirm the presence of transience in New Caledonia (Madon 2010, Constantine *et al.* 2012).

Many studies on humpback whales suggest that males and females have different behavior and capture probabilities on breeding grounds (Smith *et al.* 1999, Garrigue *et al.* 2004, Madon 2010). Therefore, to highlight the transient

Table 2. Estimated population size $\hat{N}_t$, transience-corrected estimated population size $\hat{N}_t^*$, and corresponding 95% confidence intervals (CI) using photo-identifications and genetic data for females and males between 1999 and 2005.

	Photo-identification				Females by genetics				Males by genetics			
Year	$\hat{N}_t$	CI	$\hat{N}_t^*$	CI*	$\hat{N}_t$	CI	$\hat{N}_t^*$	CI*	$\hat{N}_t$	CI	$\hat{N}_t^*$	CI*
2000	136	71, 259	95	55, 161	100	54, 186	34	16, 73	117	84, 161	56	24, 130
2001	182	120, 275	132	67, 260	150	80, 280	60	37, 98	188	136, 259	92	44, 195
2002	129	75, 221	105	52, 213	93	50, 173	41	21, 81	58	42, 81	34	16, 72
2003	179	117, 275	139	65, 297	157	84, 293	67	43, 106	154	111, 213	91	48, 171
2004	340	164, 706	253	133, 484	79	42, 146	36	17, 76	42	30, 58	25	10, 59
2005	256	148, 445	198	81, 485	171	92, 319	81	58, 114	125	90, 173	76	41, 143

behavior of males and females, we displayed the results of the genetic analyses using a model not fully supported by AICc but incorporating a sex effect because the simple model without sex effect did not allow us to develop our analysis. The sex effect could be hidden in the photographic data set due to the inability to determine sex. Based on the genetic data, the results suggest that females were more likely to be transient than males in the southern lagoon. This is surprising because female humpback whales are usually believed to be faithful to breeding grounds. Besides, Valsecchi *et al.* (2010) recently hypothesized that in order to maximize mating opportunities, the movements of males in tropical and through migratory latitudes could be more extensive than currently believed. Such a movement is supported by the transmission of humpback whale songs eastward through the populations in the western and central South Pacific recently highlighted by Garland *et al.* (2011). Moreover, the data available on the few sexed whales that moved between the wintering grounds of Oceania during the period from 1999 to 2004 revealed seven males for three females (Garrigue *et al.* 2011). All of this contributes to explain the transience observed for the males. On the other hand, females also undertake long distance movement and the longest distance reported is actually from a female (Stevick *et al.* 2010). In this context, the proportion of females being transient might not seem unusual: potential explanations of this transiency phenomenon include their behavior on breeding grounds, which makes them harder to capture (Smith *et al.* 1999, Garrigue *et al.* 2004, Madon 2010), their residency time on the breeding ground, which is much shorter than for males (Palsbøll *et al.* 1997, Craig *et al.* 2001), and the fact that some might not undertake migration or reach breeding areas every year (Brown *et al.* 1995, Craig and Herman 1997). Despite its existence, the low rate of movement between the Oceania breeding grounds actually sampled (Madon 2010, Garrigue *et al.* 2011) does not seem sufficient to explain a transiency on such a scale as suggested by our analysis. Nevertheless, the movements of individuals observed between auxiliary breeding sites such as the new off-shore habitat recently discovered in New Caledonia (Garrigue *et al.* 2010, 2011) could result in a certain amount of transiency.

Our study suggests that transients might be more available for genetic sampling than for photo-identification. This might be due to more heterogeneous capture probabilities in the genetic data set, in which case correcting for transients would reduce the downward biases on population size estimates.

Transience could also be induced by a heterogeneous sampling effort between years, and years 2002 and 2004 (Table 1) present a significantly lower sampling effort due to bad weather and unavailability of researchers in most of the season in 2004. However, there is very little chance that the transience is due to two years out of seven. If it was the case though, this heterogeneity in sampling effort could lead to heterogeneous capture probabilities for the residents, leading again to an underestimation of the resident population.

The transience signal in the genetic data set could arise from laboratory errors. Such errors could create the appearance of new individuals corresponding to what Creel *et al.* (2003) referred to as “ghost” because their genotypes do not exist. These “ghosts” would have a very low probability of recapture because it is very unlikely that another error would lead to the incorrect genotypes again. However, the low rate of measured genotyping error and the review of “near matches” (*i.e.*, genotypes differing at one or two loci) of our data set argue against this as a contributor to a signal of transience in this study. In photo-matching, having a team of experienced people and good-quality photographs will reduce the matching error rate. With natural marking, no data set is error-free but conducting parallel analysis of photo-identification and genotyping records, as this has been done here, will contribute to detecting and correcting missed photo-identifications. Photo and genetic comparisons can also inform about incorrectly assigned samples in the field. The QC processes were developed to reduce the possibility of failure to resight an individual due to the quality of the identification data. Another explanation for the significance of test 3.SR rather than the presence of transients would be large differences in survival among residents. Juveniles are thought to have a lower survival rate than adults (Reilly 1984) and their inclusion could therefore result in a downwards bias of adult survival estimate. In our data sets, juveniles as ascertained from their relative size could not represent more than 8% and 9%, respectively in photographic and genetic data sets, which could not explain transience to such an extent. The high survival generally found for all ages in this species (*e.g.*, Chittleborough 1965, Barlow and Clapham 1997, Chaloupka *et al.* 1999, Mizroch *et al.* 2004, Ramp *et al.* 2010), is similar to the one recently calculated for Oceania (Constantine *et al.* 2012) and would not explain the disappearance of many newly marked individuals out of the study area. The population under study is one with an IUCN Endangered status (Childerhouse *et al.* 2008) and while causes of the limited observed recovery are not known, population-specific impacts on survival are not impossible. In the context of abundance estimation, the uncorrected population sizes include resident and transient animals, which could lead to misinterpreting the results.

In the present study these two groups of whales are using a common area defined as the southern lagoon of New Caledonia. One contains individuals generally faithful to the southern lagoon and coming back regularly to the area, *i.e.,* the residents, whereas the other group contains transient individuals just passing through the area once. Of course the group containing transient individuals can also include resident whales with short stay durations within the southern lagoon, hence with lower annual capture probabilities. Even if it is more likely that the short stay duration on the breeding ground is due to the reproductive status (*e.g.,* gestating females arriving late on the breeding ground) and may not be a systematic behavior, further studies are needed in New Caledonia on the stay duration (Pledger *et al.* 2009) to improve our knowledge of whales movement in this region. Misclassification of residents as transients would lead to an overestimation of the transient proportion among the unmarked τ which in turn would lead to an underestimation of the resident population. However, as the number of capture occasions increases, the number of recaptures should also increase and the chance of not recapturing residents should decrease.

Our current understanding, acknowledging the presence of transients, highlights a more complex structure of the New Caledonian breeding ground than previously thought. It might also suggest that the southern lagoon, which is at present the primary sampling site, is not actually the main breeding site in New Caledonia. Until further studies clarify how these breeding sites are interconnected and used by the humpback whales in New Caledonia, it seems advisable to correct the southern lagoon population size estimates to account for transients. We encourage researchers studying populations where transients might be present to report more reliable abundance of resident populations by correcting for transients as shown in this paper.

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Supporting Information[2]

The following supporting information is available for this article online:

Appendix S1. Time-dependent two-age-class “2a” models: $\{\phi(\mathrm{a2./.})p(.)\}$, $\{\phi(\mathrm{a2./.})p(t)\}$, $\{\phi(\mathrm{a2}t/.)p(t)\}$, $\{\phi(\mathrm{a2}t/t)p(t)\}$, $\{\phi(\mathrm{a2g/.})p(\mathrm{g})\}$, $\{\phi(\mathrm{a2g/.})p(.)\}$ where ϕ is the survival rate, p the capture probability, a dot denotes no time effect, g denotes the covariate “sex” and “*t*” implies time variation.

Appendix S2. R codes for the bootstrap to estimate of the standard error of the transience-corrected population size

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