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ORIGINAL ARTICLE

Testing for the effect of meteorological conditions on transient dynamics of a reed warbler *Acrocephalus scirpaceus* population breeding in northern Iberia

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Abstract

Transients can have a severe impact on demographic parameter estimates. For instance, the use of visual counts or number of captures at a ringing station to assess indices of abundance may result in biased over-estimates due to the presence of transients. With the aim of contributing to understand transient dynamics within the Eurasian breeding passerines, we used data collected at a ringing station (2010–2018) in a reed bed area of northern Spain designed to sample breeding reed warblers *Acrocephalus scirpaceus*. Specifically, we tested for the effect of season on the proportion of transients and explored for correlations of rainfall regimens at both the winter and breeding quarters on annual fluctuations of the proportion of transients. The proportion of transients was not constant across the season; it showed relatively small values until mid-June, coinciding with arrivals from Africa and the peak of the breeding period, and then increased very steeply (means > 60%) already in July, with even ca. 90% of transients captured during the second half of July, coinciding with an influx of birds that would be already passing through the area en route to winter quarters in Africa. Analyses to estimate population trends of breeding reed warblers should take this circumstance into account; otherwise, models may show odd patterns, due to a mixture of local and non-local population that might show dissimilar demographic trends. Limiting data analyses to the breeding sub-period having a lesser amount of transients is recommended. Annual fluctuations in the proportion of transients did not correlate with any of the rainfall values in Africa (winter quarters) or meteorological conditions in Europe (NAO index; rainfall values at a local level), though it might be that we did not choose the appropriate variable/period/location combination. Our data set was relatively small; hence, this may hamper us to detect weak linear trends. Future research should contribute to answer this question and deep into the factors driving transience dynamics in bird populations.

Keywords *Acrocephalus scirpaceus* · Cormack–Jolly–Seber models · Population dynamics · Rainfall · Ringing · Transience

Zusammenfassung

Effekte von Witterungsbedingungen auf die Dynamik der Durchzügler in einer im Norden Spaniens brütenden Teichrohrsänger *Acrocephalus scirpaceus* Population

Durchzügler können gravierende Auswirkungen auf die Schätzung demografischer Parameter haben. So kann zum Beispiel die Verwendung von Zähldaten oder die Anzahl von Fängen an einer Beringungsstation für Bestandsabschätzungen aufgrund

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der Anwesenheit von Durchzüglern zu einseitigen Überschätzungen führen. Mit dem Ziel, allgemein zum Verständnis der Durchzüglerdynamik bei in Eurasien brütenden Sperlingsvögeln beizutragen, nutzten wir Daten einer Beringungsstation (2010-2018) in einem Schilfgebiet im Norden Spaniens, die für die Erfassung von brütenden Teichrohrsängern *Acrocephalus scirpaceus* konzipiert wurde. Insbesondere wurden der jahreszeitliche Effekt auf den Durchzügleranteil und mögliche Zusammenhänge zwischen Niederschlagsmengen in den Winter- und Brutquartieren und den jährlichen Schwankungen beim Durchzügleranteil untersucht. Der Anteil an Durchzüglern war nicht über die Saison hinweg konstant. Bis Mitte Juni war eine relativ geringe Anzahl zu beobachten, was mit dem Ankunftszeitpunkt aus Afrika und dem Höhepunkt der Brutsaison zusammenfiel. Bereits im Juli stieg der Durchzügleranteil dann steil an (Mittelwerte > 60%), sogar bis zu einer Fangquote von ca. 90% an Durchzüglern während der zweiten Julihälfte. Dies überschnitt sich mit dem Zuzug von Vögeln, welche dieses Gebiet bereits *en route* passierten, um ihre Winterquartiere in Afrika zu erreichen. Bei Analysen zur Schätzung der Populationsentwicklung der brütenden Teichrohrsänger sollten diese Umstände berücksichtigt werden. Ansonsten könnten aufgrund der Mischung aus lokalen und nicht-lokalen Populationen, die möglicherweise unterschiedliche demographische Entwicklungen zeigen, Modellrechnungen zu fragwürdigen Mustern führen. Wir empfehlen daher, Datenanalysen auf die Brutzeit zu beschränken, zu der nur eine geringere Anzahl an Durchzüglern vorkommt. Die jährlichen Schwankungen im Durchzügleranteil zeigten keinen Zusammenhang mit den verschiedenen Niederschlagsmengen in Afrika (Winterquartiere) oder den Witterungsbedingungen in Europa (NAO-Index; Niederschlagsmengen auf einem lokalen Level). Es könnte jedoch auch sein, dass wir nicht die geeignete Kombination aus Variablen, Zeitphasen und Orten gewählt haben. Unser Datensatz war relativ klein, sodass dies möglicherweise das Erkennen schwacher linearer Trends erschwerte. Zukünftige Studien sollten zur Beantwortung dieser Frage beitragen und sich in der Untersuchung der Faktoren vertiefen, die die Dynamik der Durchzügler in Vogelpopulationen verursachen.

Introduction

In demography, a transient is defined as an individual that spent a very short-time period at a site, which hence is left soon. Recapture models translate this fact defining a transient as an individual having zero apparent survival from a given capture event to the next one (Pradel et al. 1997). When dealing with a breeding population, transients would be those individuals which would not remain for the entire breeding season within that population (1) either because they are just passing birds that breed in other areas (e.g., in migrant species, migrants that pass over already settled, breeding populations), (2) because they fail to find a mate and hence are forced to or just leave that area, where they have been unable to breed, or (3) because some birds breed just in the edge of the net catchment area and move into the area just once (so in this case, transience is a methodological artifact) (Pledger et al. 2003). Whatever the reason, transients can have a severe impact on demographic parameter estimates (Pradel et al. 1997). For instance, the use of visual counts or number of captures at a ringing station to assess indices of abundance may result in biased over-estimates due to the presence of transients (many of the birds counted would not belong to the population for which its abundance is estimated).

The estimation of the presence and magnitude of the contribution of transients to given, local breeding populations, is still an issue poorly studied in several regions/species across Europe. In addition, even less known are still the factors driving the occurrence of transients at given sites. Which factors cause greater or lesser proportions of transients within a population? A better understanding of this aspect is called to contribute to an improvement of parameter estimates on population dynamics.

With the aim of contributing to understand transient dynamics within the Eurasian breeding passerines, we used data collected at a ringing station in a reed bed area of northern Spain designed to sample breeding reed warblers *Acrocephalus scirpaceus*. Reed warblers have a broad distribution range in Europe, where they breed in southern/medium latitudes (Cramp 1992). They overwinter in tropical Africa (Zwarts et al. 2009). Regions situated through important migratory flyways should be fairly sensitive to the presence of transients, (partly) comprised by non-local individuals still moving to their breeding areas (Arizaga et al. 2010). Therefore, it can be hypothesized that the proportion of transients should show (1) a peak early in the breeding season, when local breeding pairs (just arrived reed warblers) would mix with still migrating birds, (2) minimum values during the middle part of the breeding season (when migration ends, transients would comprise mostly local birds unable to breed), and (3) again a peak late in the season when local breeding birds mix with the first migratory birds from abroad (Pagaldai and Arizaga 2015). Apart from such seasonal dynamics, hypothesis around the yearly fluctuation of transients can also be stated. The proportion of transients could vary annually, and this may be influenced by several factors, including meteorology. Ultimate mechanisms explaining a possible relationship between weather and the proportion of transients should be expected to work via survival (e.g., through a direct effect of weather on survival or indirect effects via habitat suitability and carrying capacity)

(Newton 1998, 2013). For instance, a good (rainy) winter in Africa would allow high survival rates (Peach et al. 1991), which would result in increasing population size at breeding quarters, and this may result in a higher proportion of transients. By contrast, a dry winter may lead lower survival rates, so a lesser amount of competition at breeding quarters, which would allow all (most) birds to breed, and may then result in a lesser proportion of transients.

In this work, we tested for the effect of season on the proportion of transients in a reed warbler population from northern Iberia, and explored for correlations of rainfall regimens at both the winter and breeding quarters on annual fluctuations of the proportion of transients. The sampling site was located in the point, where the Atlantic flyway enters Iberia, between the western edge of the Pyrenees and the southeastern part of the Bay of Biscay.

Materials and methods

Sampling area and data collection

Field work was carry out at the Jaizubia stream, Txingudi marshlands (Gipuzkoa, North of Spain; 43º21′N 01º48′W), a coastal wetland located in an estuarine area (Bidasoa river mouth), at the south-eastern Bay of Biscay. The Jaizubia wetland complex occupies ca. 70 ha, out of which ca. 25 ha belong to the Jaizubia stream and its associated mudflats and reed beds.

Reed Warblers were captured from 2010 to 2018, during the months of May to August. Data were collected from the ringing campaign carried out in the area every year, based on a constant effort site oriented to catch breeding birds from May up to mid-August, with a frequency of one sampling day/fortnight (i.e., 7 ringing journeys overall). Birds were trapped with mist nets of 2.5-m high, using a total length of 228 linear meters of mist nets. Mist-netting was carried out using a constant sampling effort protocol starting at dawn up to +6 h.

Once a bird was captured, it was ringed (or its ring was read if previously ringed), and the age was determined (adults: EURING code 4; first-year birds: EURING code 3) (Svensson 1996).

Weather data were collected from three sources and regions: rainfall in tropical Africa (Sahel), rainfall at breeding quarters, and the NAO index. Rainfall data from the Sahel was obtained as an index over the mean value calculated for the period 1901-2017, for the months of June to October (source: JISAO data, https://doi.org/10.6069/h5mw2f2q). Negative values of this index show that the precipitation was below the mean and positive values show an amount of precipitation higher than the mean. This index has shown to be a good method to represent precipitation anomalies in the Sahelian belt (Becker et al. 2013; Nicholson et al. 2018), and has a very good (positive) correlation with vegetation productivity (Zwarts et al. 2009). Rainfall data from the sampling site were obtained from a meteorological station located at S. Sebastián's airport, less than 1 km from sampling site (source: AEMET, aemet.es). Finally, the NAO index was taken from the NOAA website (www.cpc.ncep.noaa.gov).

Data analyses

The data used in this work only concerned adult birds. We removed juvenile birds to focus only on breeders that, theoretically, should not exhibit the (higher) dispersal rate expected among the first-year birds.

We used Cormack–Jolly–Seber (CJS) models fitted in Program MARK (White and Burnham 1999) to estimate the presence of transients and their proportional contribution to the population. CJS models estimate survival between time intervals, t, (φ_t), and recapture probability (p) separately. When we have transients in a sample, φ(time 1) differs from φ in subsequent time intervals, and in this case, φ(time 1) < φ(time 2). The proportion of transients can be calculated as: $1-(\varphi_1/\varphi_2)$ (Pradel et al. 1997). For that goal, we built a matrix of 7 columns (one column per fortnight) × 627 rows. Years were pooled and each bird was considered once every year (i.e., each individual bird was considered as a new row every year, so overall, these 627 rows corresponded with 534 individuals). Within each year, we also calculated how many birds were captured only in that year and how many were captured in multiple occasions (years). A goodness-of-fit test ran in the Program U-CARE (Choquet et al. 2009) showed that these data set had a problem of transience (test for the presence of transients, statistics = 3.85, $P < 0.001$), and not of trap-dependence (statistics = 0.29, $P = 0.773$). With this data set, we run alternative models considering constant survival (φ), constant transience (i.e., the proportion of transients is constant across the season, notation: φ_1, φ_2), and time-dependent transience (i.e., the proportion of transients varies across the season, notation: $\varphi_{1(t)}$, φ_2). In all of the models, we forced p to be constant.

Thereafter, we built a second matrix to calculate transience estimates on a yearly basis. In this case, the matrix had 9 columns (years 2010–2018) × 534 rows (individuals). In this second analysis, we considered captures obtained for the entire sampling period within each year (i.e., up to August). Even though the proportion of transients was observed to increase in July–August as compared to the previous months (Fig. 1), we did not have enough sample size to run an analysis only considering captures before July (CJS parameter estimates showed very high standard errors, thus resulting in less precise estimates). Nonetheless, in an exploratory analysis of

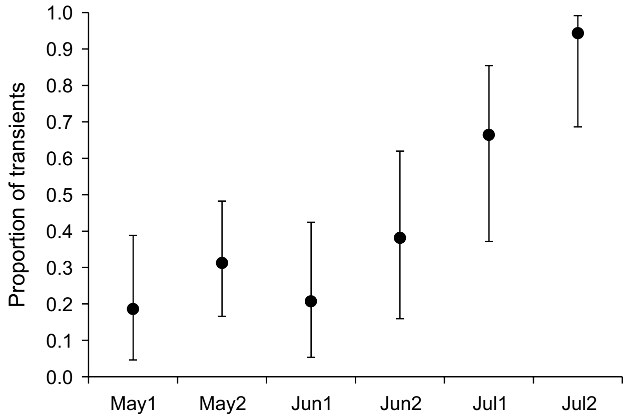

Fig. 1 Proportion of transients (±95% confidence interval) of reed warblers at Jaizubia, across breeding period. May 1 represents the proportion of transients for the time interval existing from the first half of May to the second one, and so on

the data using only the captures obtained up to June, we obtained roughly similar survival values, and more importantly, such values did not improve the correlation with an index of adult reed warblers' abundance at Jaizubia (see below for further details). Again, in this case, the data did not fully fit with the CJS models' assumptions, due to the presence of transients ($\chi^2 = 33.18$, $P = 0.010$; specific test to detect transients: statistics = 4.32, $P < 0.001$). We built alternative models considering constant survival, constant transience (i.e., the proportion of transients is constant across the season, notation: φ_1, φ_2) and time-dependent transience (i.e., the proportion of transients varies across the season, notation: $\varphi_{1(t)}$, φ_2). In all of the models, we forced p to be constant. In addition, to test for the effect of meteorological conditions (mainly rain at a number of geographic scales) on the proportion of transients, we replaced models assuming time-dependence transience by models assuming a univariate linear effect of weather-related covariates (notation: $\varphi_{1(\text{covariate})}$, φ_2): NAO index from January to August (*nao1* to *nao8*, respectively), accumulated rain at Txingudi from March to June (*rain.txin3* to *rain.txin6*), Sahelian rainfall anomaly (*rain.sahe*). Multivariate models were rejected here due to sample size constraints.

Finally, we checked whether the proportion of transients was correlated with an index of adult reed warblers' abundance at Jaizubia. We used for that the 'cesr' package (Robinson 2014) designed to analyse ringing data from a constant effort site in R (R Core Team 2014). In particular, we used the function 'index' to obtain parameter estimates of bird abundance over the entire study period (2010–2019).

Statistical analyses were conducted in MARK (White and Burnham 1999) and R (R Core Team 2014).

Table 1 Cormack–Jolly–Seber models used to test whether the proportion of transients varied across the breeding period

Models	AICc	ΔAICc	AICc weight	np	Deviance
$\varphi_{1(t)}, \varphi_2, p$	1098.15	0.00	0.998	8	95.73
φ_1, φ_2, p	1110.92	12.78	0.002	3	118.68
φ, p	1116.74	18.61	0.000	2	126.53

Results

Transients within the season

The proportion of transients was not constant across the season (Table 1). Models considering either a constant proportion of transients across the season or constant survival did not fit to the data so well. At the beginning and until the first half of June, this proportion showed mean values around 0.20–0.30 (i.e., 20–30% transients) (Fig. 1). From the second half of June onwards, however, the proportion was detected to increase very steeply, up to reaching a mean value close to 1 during the second half of July (i.e., > 90% of reed warblers captured during the second half of July were transients, so had left the area before August).

Transients between seasons

Overall, the (observed) proportion of reed warblers (captures considered here up to August) captured only 1 year ranged from 58% (in 2016) to 86% (in 2011; mean ± SD = 72.7 ± 11.5%). According to the first model the proportion of transients varied annually, but not the annual survival of the non-transient population (Table 2). This proportion of transients ranged from 0.26 (in 2016) to 0.80 (in 2011).

Single-correlation analyses revealed that the proportion of transients did not have a significant correlation with any of the meteorological variables (Pearson correlations, all P values > 0.18; for details, see Electronic Supplementary Material). In concordance with this result, any of the models assuming weather-related covariates fitted to the data better than a model considering time-dependence on transience (Table 2). The proportion of transients along the study period tended to decrease (Fig. 2a; $r = -0.47$), but the trend was, again, non-significant ($P = 0.24$).

The population of reed warblers tended to increase, though the trend was non-significant (slope: + 0.11 ± 0.08; $P = 0.311$; Fig. 2b). The proportion of transients tended to be positively correlated with an index of bird abundance, with the P value being marginally significant ($r = +0.70$, $P = 0.05$; Fig. 2c).

Table 2 Cormack–Jolly–Seber models used to test whether the proportion of transients varied annually, and whether the proportion of transients was influenced by weather-related covariates

Models	AICc	ΔAICc	AICc weight	Np	Deviance
$\varphi_{1(t)}, \varphi_2, p$	583.99	0.00	0.764	10	61.87
$\varphi_{1(t)}, \varphi_{2(t)}, p$	586.89	2.90	0.179	16	52.18
φ, p	590.01	6.02	0.038	3	82.25
$\varphi_1, \varphi_{2(t)}, p$	591.34	7.35	0.019	9	71.30
$\varphi_{(t)}, p_{(t)}$	604.86	20.87	0.000	15	72.27
φ, p	610.46	26.48	0.000	2	104.73
$\varphi_{(t)}, p$	610.54	26.56	0.000	9	90.50
Models assuming weather-related covariates on φ_1:					
$\varphi_{1(rain.sahe)}, \varphi_2, p$	590.96	6.97	0.013	4	81.17
$\varphi_{1(rain.txin3)}, \varphi_2, p$	591.99	8.01	0.008	4	82.21
$\varphi_{1(rain.txin4)}, \varphi_2, p$	591.94	7.95	0.008	4	82.15
$\varphi_{1(rain.txin5)}, \varphi_2, p$	591.93	7.94	0.008	4	82.14
$\varphi_{1(rain.txin6)}, \varphi_2, p$	591.69	7.70	0.009	4	81.91
$\varphi_{1(nao1)}, \varphi_2, p$	591.82	7.83	0.008	4	82.03
$\varphi_{1(nao2)}, \varphi_2, p$	591.12	7.13	0.012	4	81.33
$\varphi_{1(nao3)}, \varphi_2, p$	591.52	7.53	0.010	4	81.73
$\varphi_{1(nao4)}, \varphi_2, p$	590.34	6.35	0.018	4	80.55
$\varphi_{1(nao5)}, \varphi_2, p$	590.44	6.45	0.017	4	80.65
$\varphi_{1(nao6)}, \varphi_2, p$	590.89	6.90	0.013	4	81.10

Abbreviations of covariates: *nao1* to *nao6,* NAO index from January to June; *rain.sahe*, Sahelian rainfall anomaly; *rain.txin3* to *rain.txin6*, rainfall in Txingudi from March to June

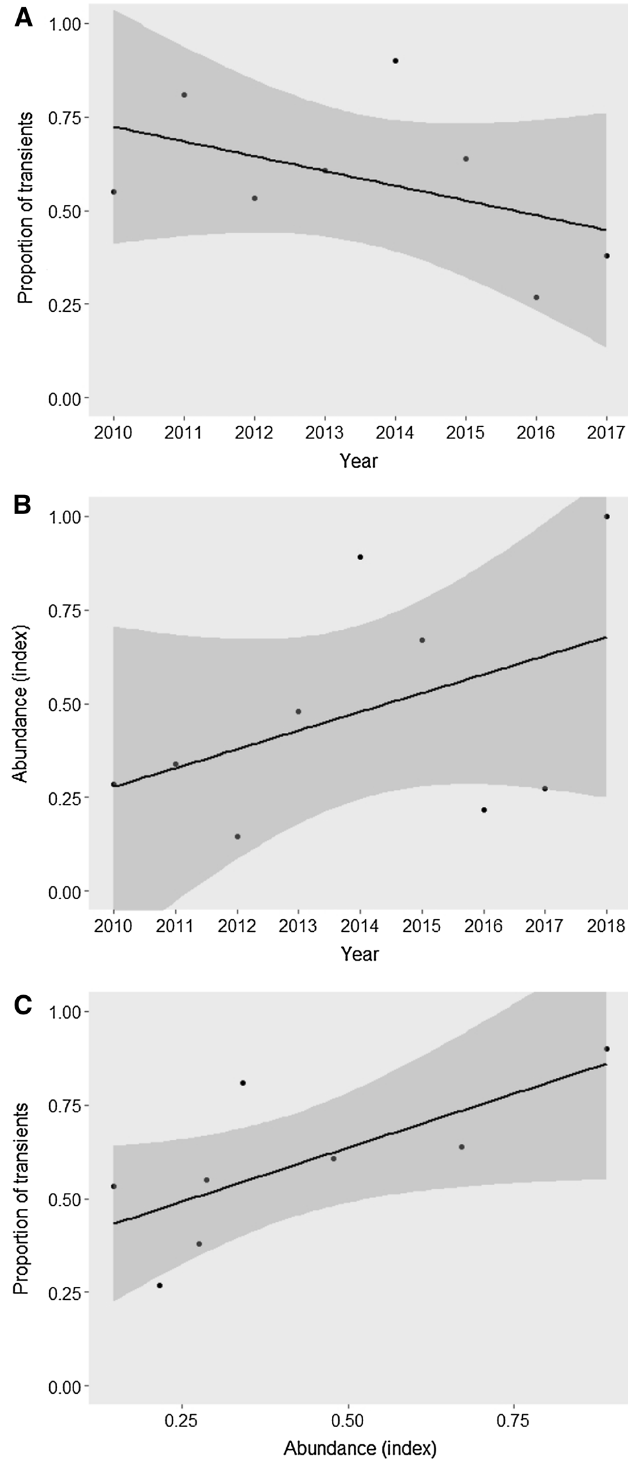

Fig. 2 Temporal trend (linear regression ± 95% confidence interval) of the proportion of transients (**a**), abundance index of adult reed warblers (**b**), and the relationship of the two variables (**c**) along the study period

Discussion

This is one of the few case studies dealing with the estimation of the presence of transients in European breeding bird populations of passerines (Johnston et al. 2016). The proportion of transients of reed warblers at a reed bed area in northern Spain varied across the breeding season. This proportion showed relatively small values until mid-June (means of 20–30%), coinciding with arrivals from Africa (Cantos 1992) and the peak of the breeding period (Pagaldai and Arizaga 2015). This result suggests that reed warblers breeding in areas located further north may not stop over within the region; otherwise, we should have detected a very high proportion of transients in the first and, maybe, the second half of May, as it is detected in late-July or August (Fig. 1). However, these means do not exclude the possibility of having days of strong passage also in May or even part of June (Arizaga et al. 2010), with the corresponding effect of increasing the proportion of transients. Previous research already revealed that the spring passage within the region was very weak, because the amount of reed warblers or other *Acrocephalus* warblers caught in the reed beds from the southeastern part of the Bay of Biscay was very low, and very marginal as compared to the bulk detected during the autumn migration period (Arizaga et al. 2014). This is, indeed, a general pattern through much of Europe (Newton 2008). The nature of these early transients still remains unknown. They did not differ morphologically from local breeding birds, but they had slightly higher fuel loads and might be either migrants or just locals arriving too late and, therefore, unable to find a mate/territory (Arizaga et al. 2010).

The presence of transients became very high (means > 60%) already in July, with even ca. 90% of transients captured during the second half of July. Such a high influx of transients was due to the income of migrants en route to winter quarters in Africa—autumn migration period—(Cramp 1992; Arizaga 2010). This result highlights that the majority of the captures obtained in July or August belong to apparently non-local birds. We consider that analyses to estimate population trends of breeding reed warblers (Peach et al. 1998; Robinson et al. 2009) should take this circumstance into account; otherwise, models may show odd patterns, due to a mixture of local and non-local population that might show dissimilar demographic trends. Noteworthy, we observed that years with more reed warblers (higher index of adult reed warblers' abundance) were also years with a higher proportion of transients. Limiting data analyses to the breeding sub-period having a theoretically lesser amount of transients (e.g., in this work captures of May to June), however, does not seem to solve this problem totally, because we can still find years with a very high proportion of transients. Alternatively, an index that would be controlled for the proportion of transients (or that would only consider adult birds with signs of being breeding, such as brood patch or cloacal protuberance) should provide better estimates of the non-transient population size.

Annual fluctuations in the proportion of transients did not correlate with any of the used rainfall values in Africa (winter quarters) or meteorological conditions in Europe (NAO index; rainfall values at a local level). Therefore, it remains unknown whether meteorological conditions may have any influence on transient dynamics. Our data set was relatively low ($n = 9$ years), and this may hamper us to detect linear trends that, with a larger data set, may be significant. Moreover, given the complex effects of weather variables on bird populations, we cannot reject the fact that we did not choose the adequate variables/periods/locations (Haest et al. 2018a, b, 2019).

The proportion of transients tended to decrease along the study period, though the slope was non-significant. The decrease was observed to be most noticeable in the last 2 years (mean of 0.32 as compared to a mean of 0.68; Fig. 2). This decreasing amount of transients in these 2 years may be due to different biological phenomena, such as a higher mortality during the winter affecting the transient population or a decreasing use of the area by transients in spring. All this is speculative, but it is mentioned here to open discussion and encourage future potential research that should contribute to answer this question and deep into the factors driving transience dynamics in bird populations.

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