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Title	Acoustic activity across a seabird colony reflects patterns of within-colony flight rather than nest density
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Publication date	2019-05-18
Original Citation	Arneill, G. E., Critchley, E. J., Wischnewski, S., Jessopp, M. J. and Quinn, J. L. (2019) 'Acoustic activity across a seabird colony reflects patterns of within-colony flight rather than nest density', Ibis, 162(2), pp.416-428. https://doi.org/10.1111/ibi.12740
Type of publication	Article (peer-reviewed)
Link to publisher's version	https://onlinelibrary.wiley.com/doi/abs/10.1111/ibi.12740 - 10.1111/ibi.12740
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Download date	2026-11-07 01:40:44
Item downloaded from	https://hdl.handle.net/10468/8320

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Accepted Article

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Article type : Original Paper

Editor: Pichegru, Lorien

Running head: *Within-colony flight influences biophony*

Acoustic activity across a seabird colony reflects patterns of within-colony flight rather than nest density

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Passive acoustic monitoring is increasingly used as a cost-effective way to study wildlife populations, especially those that are difficult to census using conventional methods. Burrow-nesting seabirds are amongst the most threatened birds globally, but they are also one of the most challenging taxa to

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/ibi.12740

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census, making them prime candidates for research into such automated monitoring platforms. Passive acoustic monitoring has the potential to determine presence/absence, or quantify burrow-nesting populations, but its effectiveness remains unclear. We compared passive acoustic monitoring, tape-playbacks, and GPS tracking data to investigate the ability of passive acoustic monitoring to capture unbiased estimates of within-colony variation in nest density for the Manx Shearwater *Puffinus puffinus*. Variation in acoustic activity across twelve study plots on an island colony was examined in relation to burrow density and environmental factors across two years. As predicted fewer calls were recorded when wind speed was high, and on moon-lit nights, but there was no correlation between acoustic activity and the density of breeding birds within the plots as determined by tape-playback surveys. Instead, acoustic indices correlated positively with spatial variation in the in-colony flight activity of breeding individuals detected by GPS. Though passive acoustic monitoring has enormous potential in avian conservation, our results highlight the importance of understanding behaviour when using passive acoustic monitoring to estimate density and distribution.

Keywords: passive acoustic monitoring, acoustic indices, census methods, telemetry, burrow-nesting seabird, procellariiformes

Time and cost-efficient methods for censusing and monitoring populations are highly sought after in conservation (Wätzold & Schwerdtner 2005, Nichols & Williams 2006). Automated monitoring platforms are becoming increasingly important because they lower cost, whilst reducing observer bias and disturbance (Carey 2009). Passive acoustic monitoring has been widely used in both terrestrial and marine ecosystems, especially on vocally active, cryptic species such as cetaceans (Mellinger *et al.* 2007, VanParijs *et al.* 2009, Borker *et al.* 2014). The large distances that underwater vocalisations travel advocates the use of passive acoustics in the marine environment, allowing the measurement of patch usage and presumed habitat quality in vocalising species (Verfuß *et al.* 2007,

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Pirotta *et al.* 2014). The general effectiveness of acoustic monitoring remains far from clear, however, for a wide variety of reasons. For example, species differ in critically important factors, including call frequency, call amplitude, and call directionality, all of which influence detectability. Furthermore, determining exactly what area is being sampled and how detectability changes with distance from the centre of the sample plot is extremely challenging (Robbins *et al.* 2015, Dufour *et al.* 2016). Thus there is a pressing need for further studies in a broader range of taxa before the full potential of passive acoustic monitoring can be realised.

Despite the limited distances over which sound travels in air, researchers have used passive acoustic methods to study a wide range of questions among avian species in terrestrial ecosystems. These range from behavioural studies on vocal communication (Crane *et al.* 2016) and sexual selection (Taff *et al.* 2014), to the identification of new species (McKay *et al.* 2010). One group that has proven particularly suitable for passive acoustic studies are seabirds. Across several species, seabird vocalisations have been used to make inference on key characteristics of the emitter, including sex (Curé *et al.* 2012), body size (Favaro *et al.* 2017) and individual identity (Mathevon *et al.* 2003). Furthermore, the colonial nature of most seabirds potentially makes the use of passive acoustic monitoring a cost-effective tool, increasing efficiency in collecting data across multiple colonies over a large geographical scale, determining species assemblages and numbers, and estimating breeding parameters such as phenology (Borker *et al.* 2015, Frommolt *et al.* 2017). As a result, passive acoustic monitoring has been used to examine the efficacy of island-population restoration efforts (Buxton & Jones 2012, Croll *et al.* 2016), determine colony attendance (Mckown 2008), and estimate population size (Oppel *et al.* 2014).

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Seabirds are amongst the most threatened taxa globally, with declining population trends observed across the majority of monitored species due to various anthropogenic pressures (Croxall *et al.* 2012, Paleczny *et al.* 2015). Yet, for many burrow-nesting seabirds, fundamental demographic data is not available to accurately define the conservation status of populations (Paleczny *et al.* 2015). This is largely because many are difficult to census due to their low detection probability in breeding colonies, being visually inconspicuous while in their burrows or only returning to the colony at night. Census methods are laborious, often requiring individual burrows to be assessed by visual inspection or tape-playbacks to determine the number of breeding pairs within the narrow window of incubation and chick-guarding when birds respond to tape-playbacks (James & Robertson 1985, Mitchell *et al.* 2004). However, an increased use of vocalisations at night-time when many burrow-nesters return to the colony (Brooke, 1986) suggests passive acoustic monitoring could be an effective method of estimating the local density of birds breeding within an area. Oppel *et al*. (2014) used passive acoustic monitoring to establish a relationship between acoustic activity in Cory's Shearwaters *Calonectris borealis* and nest density around recorders. Recorders were then deployed in other areas to estimate variation in density within difference habitats across a colony. The findings were then used to estimate population size by extrapolating the predicted densities across the entirety of these different habitats. Despite the potential for the approach, the ability of passive acoustic monitoring to capture unbiased estimates of within-colony nesting density remains scarcely examined.

The effectiveness of passive acoustic monitoring to estimate the local density of breeding birds will be influenced by the presence, and interactions of, various sources of human-related ('anthrophony'), geophysical ('geophony') and biological ('biophony') sounds within the soundscape (Mazaris *et al.* 2015, Gasc *et al.* 2017). Therefore, sources of anthrophony and geophony should be considered when studying the biophonic component of a soundscape. The remote nature of many seabird breeding colonies likely reduces the influence of anthrophony, allowing acoustic indices such as the Acoustic

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Complexity Index (ACI) to assess biophony independent of anthrophony (Pieretti *et al.* 2011). In many seabird colonies, the close proximity to the coast will be associated with increased geophony in the soundscape (e.g. offshore winds), often reducing the quality of recordings (Buxton & Jones 2012). Furthermore, avian species are known to alter their vocal behaviour in response to high levels of anthrophony (Slabbekoorn & den Boer-Visser 2006) and geophony (Gasc *et al.* 2017), some calling less (Lengagne & Slater 2002) or more (Lengagne *et al.* 1999) frequently. A species' vocal behaviour may also be influenced by other inaudible environmental factors, for example in some burrow-nesting seabirds, periods of high moon illumination are associated with reduced attendance within the colony (Buxton & Jones 2012, Oppel *et al.* 2014). The importance of controlling for these factors that affect the soundscape, and the detectability of a species' vocalisations, has been discussed in detail within the literature (Buxton & Jones 2012, Oppel *et al.* 2014) and should be considered when studying biophony within a soundscape.

The biophonic component of the soundscape is expected to be influenced not only by the number of vocalising birds within the colony, but also by the species' behaviour. One reason for this is that many of the vocalisations recorded may be caused by non-breeders (James, 1985). Another behaviour that may influence the soundscape is the movement of birds within the colony. This may be a key factor shaping the soundscape of seabird colonies, as individuals within a colony are known to follow conspecifics between breeding sites and rafts or foraging grounds at sea (Weimerskirch *et al.* 2010, Meier *et al*. 2015, Jones *et al*. 2018). Such behaviour results in defined routes, or corridors, that are used by many individuals within the colony (hereafter 'flight paths'). Although telemetry studies have been widely used to study the behaviour and fine-scale distribution of individuals at sea (Nesterova *et al.* 2015, Burger & Shaffer 2008, Lascelles *et al.* 2016), to our knowledge it has never been used to understand the biophony within a soundscape and the effectiveness of passive acoustic monitoring within a seabird colony.

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In this study we examine the relationship between the biophonic component of the soundscape and the within-colony variation in the local nest density of breeding Manx Shearwaters *Puffinus puffinus*. This species is a burrow-nesting procellariform that predominantly breeds in large colonies on remote offshore islands across the North Atlantic. It returns to the colony only at night for incubating change-overs or chick provisioning, is highly vocal and rarely censused (Mitchell *et al.* 2004). We combine passive acoustic monitoring and plot census surveys using tape-playback methods to determine whether acoustic activity is related to the local density of breeding birds within a colony. We examined acoustic activity within the biophonic component of the soundscape using both (a) the automatic detection of species-specific calls and (b) two acoustic indices known to be good metrics for studying avian abundance, the ACI and the Bioacoustic Index (BIO; Boelman *et al.* 2007). Testing this relationship across acoustic analyses techniques allowed us to draw conclusions on the ability to estimate the local density of Manx Shearwaters within an area using passive acoustic monitoring. We predicted that areas with a high density of breeding birds will be correlated with higher acoustic activity. Finally, to test if movement of breeding birds within the colony influenced the biophonic component of the soundscape, we looked at the frequency and consistency of flight paths through these study plots using data obtained from GPS tagged Manx Shearwaters. We predicted that birds flying within the colony would contribute to biophony within the colony soundscape.

METHODS

Density and distribution of Manx Shearwaters

Our study site was High Island, Co. Galway, off the west coast of Ireland (53.54663N, -10.2573W) where the density and distribution of breeding Manx Shearwaters was known from previous whole island surveys using tape-playback (Arneill 2018). Tape-playback methods involve playing the call(s)

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of a conspecific to evoke a behavioural response (Walsh *et al.* 1995). Used across several species (Ratcliffe *et al.* 1998, Rayner *et al.* 2008, Bolton *et al.* 2010, Perrins *et al.* 2012), tape-playbacks provide a count of 'apparently occupied' burrows if a response is elicited. Some aspects of this methodology vary with respect to species-specific behaviours. Here, calls from multiple male Manx Shearwaters recorded on Skokholm (Xeno-canto.org) were played at burrow entrances at a natural volume (ca. 55dB) for three to four call cycles (ca. 15 seconds), or less if an immediate response was received (Smith *et al.* 2001). The call was played at a natural volume to ensure that (i) the call is loud enough to evoke a behavioural response and (ii) that the observer can hear any elicited response. Male recordings were used because they are known to elicit a higher number of responses (but see Perkins *et al.* 2017). Survey efforts were carried out during the incubation period as many adults are not present in the burrow post chick-guarding stage (Brooke 1986) and therefore would not respond to tape-playback.

Since not all birds respond to tape-playbacks, the response rate, known as the proportion of responses from nests that are known to be occupied must be calculated and applied to the number of responses elicited during the tape-playback survey. This response rate was calculated following methods outlined in Smith *et al.* (2001) and Perrins *et al.* (2012). Specifically, tape-playbacks were carried out across a series of four trials on 33 and 48 burrows within the colony that were known to be occupied in 2015 and 2016, respectively. The mean proportion of responses received and variation across trials are then used as the local response rate, which were 0.51 (SE ± 0.015) and 0.40 (SE ± 0.016) in 2015 and 2016, respectively. Tape-playback trials carried out to obtain the response rate used a total of seven recordings in a randomised order to reduce simple pseudoreplication (Kroodsma *et al.* 2001), and were separated by 24 hours to reduce the risk of habituation.

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Acoustic recording

Several previous studies in closely related procellariforms, with similar call amplitudes and breeding habitats, found that Wildlife Acoustic's Song Meter units can record vocalisations up to 50 metres away (Buxton & Jones 2012, Oppel *et al.* 2014, Dufour *et al.* 2016). In 2015 and 2016, acoustic recorders (Wildlife Acoustic SongMeter 3 in 2015 and Wildlife Acoustic SongMeter 4 in 2016) were deployed across 12 study plots representing a range of Manx Shearwater densities within a 50 m radius of recorders (Fig. 1, Table 1). Recorders were placed on an 80 cm wooden stake driven into the centre of the plots. Recorder height was approximately 50 cm above the ground to ensure the recorder stood above the vegetation across all study plots. In 2015, two recorders were available, and these were moved in a random order across the 12 study plots in cycles of six nights. These cycles were carried out non-consecutively across the breeding season from the 25th of May to the 23rd of August when fledging began. The addition of 10 extra acoustic recorders in 2016 enabled concurrent monitoring across all 12 study plots to collect comparable data between the 8th of June and 24th of August non-consecutively. All recorders were programmed on identical cycles, where constant recordings were taken between 23:00 and 04:00 when birds are known to be most active in the colony (Brooke 1978). The gain and sample rate of each recorder was +42.0 dB and 16 kHz, respectively, as default settings.

Telemetry

GPS tags (i-gotU GT-120, Mobile Action Technology, Taiwan) were deployed on 5 breeding Manx Shearwaters in 2014, 36 in 2015, and 9 in 2016. Birds were tracked during chick rearing in 2014, 2015 and 2016, and additionally during incubation in 2015. GPS tags were attached using a temporary attachment method (Tesa® 4651, tesa GmbH, Hamburg, Germany) to the mantle feathers and removed on return of the bird to the colony. Birds were weighed before tag deployment, and tags were only deployed when the device weight (13-17g depending on battery configuration) was

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within 4% of the bird's body weight. Deployments lasted several days and there was no detectable device effect on the welfare of both the tagged adults and their chicks (see Wischnewski *et al*. 2019). All telemetry work was conducted under licence by the British Trust for Ornithology (BTO) and the National Parks and Wildlife Service. Sampling intervals of GPS tracks differed between incubation and chick rearing, incubation trips recorded fixes every 8 or 12 minutes while chick rearing recorded fixes at 4-minute intervals. The distribution of nests from which GPS tags were deployed and the distribution of breeding Manx Shearwaters on High Island are shown in Figure 1. GPS tracked birds were distributed in an area that hosted >80% of the breeding colony (Fig.1). The large sample size of GPS tracks, combined with the patchy distribution of the colony and consistency of flight paths across years gives us confidence that these flight paths are representative of in-colony flight across High Island.

We analysed GPS data from 2015 and 2016 to explore in-colony flight and its relationship with acoustic activity in the same years. Specifically, we looked at the number of times individual tracks intersected each of the acoustic study plots (circular plot with radius of 50 m) using ArcGIS (ESRI, version 10.3.1**)** (Fig. 1), and compared this with the average acoustic activity at each plot using a Spearman's rank correlation test. To assess consistency in flight paths and space use in relation to the location of acoustic recorders, Dutilleul's modified t-tests (Dutilleul *et al*. 1993) that account for spatially autocorrelated data were carried out across all three years (2014, 2015 and 2016) of telemetry data.

Acoustic analyses - automatic detection of calls

Manual segmentation was carried out to provide training vocalisations that were later used in the automated extraction of signals from all data using the Wildlife Acoustics Song Scope software (©

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2017 WILDLIFE ACOUSTICS, INC.). Manual segmentation of data consisted of the visual inspection of time-frequency spectrograms of twenty randomly selected recordings across various acoustic backgrounds; these segments were inspected using the Audacity 2.1.2 software (© 2018 Audacity Team). Manual segmentation was used to reduce the number of false positive detections and to limit false negatives where detections were missed (Dufour *et al.* 2016). Measured signals were combined with five high-quality pre-recorded reference calls to enhance the accuracy of the call recognition model; these recordings were obtained from Skokholm (Xeno-Canto.org), and manually recorded calls from High Island and Great Blasket, Co. Kerry. As the repertoire of the Manx Shearwater is limited to just one major call type, comprised of one inhalant note and one exhalent note (James 1985), recognition models could be built with a high degree of accuracy on these sampled recordings. Song Scope requires several optimal model parameters that were obtained from the various recordings manually segmented as above. These parameters include: frequency range; minimum frequency; maximum syllable duration; maximum song duration and sample rate (Hz); Fast Fourier Transform window size (FFT); dynamic range and maximum Hidden Markov Model (HMM) states.

Once created, recognition models ran through all data across both years. To reduce the number of false positives, identified calls were discarded where the quality score of recognised calls was < 60. False negative calls, defined as calls that possessed all frequency characteristics but were missed by the recognition model, were identified as outlined by Buxton and Jones (2012), with a randomly selected 15 minutes of recording visually scanned from each recording hour within each plot from each year. False negatives provide a measure of model accuracy across novel data, identifying conditions in which the recognition model's performance is favourable (lower number of false negatives) or limited (higher number of false negatives). Visual scans were restricted to recordings where calls could be distinguished from background noise on spectrograms. The 15-minute samples

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were extracted from the 850 hours of recording, approximating 23% of data. Environmental conditions, such as wind speed affect the number of false negatives (Buxton & Jones 2012); therefore we report the false negative rates across three different categories of wind speed (0-10 knots, 10-20 knots, 20-30 knots; Supporting Information Table S1).

Acoustic analyses - acoustic indices

To further investigate the relationship between biophony from passive acoustic monitoring and local nest densities estimated from tape-playbacks, two acoustic indices were calculated for each recording. In our study site, the biotic component of the soundscape was almost entirely composed of Manx Shearwater vocalisations as the site only hosts one other large breeding population, European Storm Petrels *Hydrobates pelagicus* (Arneill 2018). This species is less vocal within the colony as it relies primarily on other navigational cues (Mínguez 1997). Thus, we assume that variation in these indices of the biophonic component of the soundscape largely reflects variation in Manx Shearwater vocalisations. The ACI (Pieretti *et al.* 2011) and BIO (Boelman *et al.* 2007) are known to be correlated with the number of vocalisations produced by a bird community, and were calculated using the *multiple_sounds* function in the soundecology package in R (Villanueva-Rivera & Pijanowski 2018). Package default settings were used with the exception of the frequency limits for biophony, set to 1.5-8 kHz, 500 Hz lower than the package default (2 kHz) to ensure the range of the Manx Shearwater call was included in the biotic component of the analyses. ACI results reported by the soundecology package are accumulative, values were divided by the number of minutes within each recording (60) to provide values that are easier to compare (Villanueva-Rivera & Pijanowski 2018).

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Data analysis

Analysis of the relationships between calls per hour, burrow density and environmental data were carried out using a zero-inflated negative binomial mixed model in the R package glmmADMB (Bolker 2006). This model was used to account for over-dispersion due to the large numbers of zero values and positive integers, where the dispersion statistic theta (θ) was greater than 15 in all models. Plot was included as a random effect to account for repeated measures at each of the plots. Hourly environmental data including wind speed and cloud cover were sourced from weather stations within 100 km of the study site (Met Éireann), while nightly moon illumination data was sourced from the US Naval website (https://aa.usno.navy.mil/data/docs/MoonFraction.php). These environmental covariates were included as they are known to affect the quality of recordings (wind) and the attendance within the colony (moon illumination and cloud cover). Recording hour was included as a factor to determine any variation in the number of calls throughout the night. To remove zero-inflation, potential variability in the number of calls between hourly recordings, and the lack of variability across hours in the nightly moon illumination data, data were also aggregated at the nightly scale and modelled using a negative binomial mixed model in the R package glmmADMB. Using the same covariates, the same relationships were explored using the biophony scores of each acoustic index (ACI and BIO) using generalised linear mixed models (GLMM), with a Gamma error structure and log-link. Models were compared using both AIC and BIC values, and likelihood-ratio tests to determine the model with the best fit.

RESULTS

Automatic detection of calls

A total of 850 hours of recordings were obtained from the two years across the 12 study plots, and a total of 24,502 calls were identified using the Song Scope recognizer. The number of calls (hereafter

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reported as 'calls per hour/night') is the number of vocalisations detected in the recordings by the automated recognition model. The mean number of calls per hour ranged from 9.55 to 87.05 and from 2.86 to 70.3 across the 12 study plots in 2015 and 2016, respectively. The Song Scope recognition model performed with an accuracy of 75.4% ± 3.37% across all training data. Overall, the performance of the recognition model was affected by increased wind speed (see Supporting Information Table S1, $P < 0.001$, *effect* = 1.147 (± 0.24), $n = 840$).

Temporal and Environmental variation in acoustic activity

Here, we report the temporal and environmental variation in acoustic activity, with specific reference to the calls per hour, calls per night, ACI and BIO where appropriate. During the incubation period, acoustic activity was higher compared to the chick-rearing stage (Tables 2 and 3). Acoustic activity was lower in the hour before midnight (23:00-00:00) compared to all other recording hours (00:00 – 04:00) in both years (Tables 2 and 3). Across all measures, acoustic activity was lower in 2016 than in 2015 (Tables 2 and 3).

Acoustic activity also varied with the environmental variables. First it decreased with wind speed (Tables 2 and 3), which as expected agrees with an increase in the number of false negatives with wind speed (see Supporting Information Table S1). Acoustic activity also decreased with moon illumination (Tables 2 and 3). Cloud cover had no significant effect on the number of calls per hour, calls per night or BIO (Tables 2 and 3). Cloud cover, and an interaction between cloud cover and moon illumination, had a significant effect on the biophony of ACI (Table 3), whereby acoustic activity was greater on nights with increased cloud cover, even when moon illumination was high.

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Relationship with density and flight paths of breeding Manx Shearwaters

None of the acoustic activity measures predicted local burrow density (Tables 2 and 3; Fig. 2 and Fig. 3). The number of times GPS tracks intersected the acoustic monitoring plots was positively correlated with acoustic activity; while the *p* values were not significant when this was assessed using the number of calls detected (calls per hour: rho = 0.49, $P = 0.1098$, $n = 12$; calls per night: rho = 0.49, $P = 0.11$, $n = 12$; Fig. 3), they were significant when acoustic activity was measured by the acoustic indices (ACI: rho = 0.57, $P = 0.05$, $n = 12$; BIO: rho = 0.59, $P = 0.04$, $n = 12$; Fig. 2 and Fig. 4). In the preceding analyses, one data point had high leverage ($D_i = 0.71$) with a particularly low number of intersecting tracks and relatively high acoustic activity. This was from a plot close to the tagging location, where the number of intersections were underestimated due to a combination of (i) GPS fixes not being taken when birds are underground in the burrow, therefore tracks terminated outside of the 50 m radius of the plot, and (ii) tracks originating or terminating in the area only intersect the plot once resulting in very few 'transitions' through the area. Removing this plot from the analyses reduced the *p* values further (calls per hour: rho = 0.6, $P = 0.056$, $n = 11$; calls per night: rho = 0.55, $P = 0.08$, $n = 11$; ACI: rho = 0.66, $P = 0.03$, $n = 11$; BIO: rho = 0.73, $P = 0.01$, $n = 11$; Fig. 4). Dutilleul's modified t-tests showed that the number of track intersections occurring across plots was highly consistent across years, with correlation values ranging from 0.9967 to 0.999 ($P < 0.001$).

DISCUSSION

Monitoring wildlife populations is extremely labour intensive and considerable effort is put into identifying efficient automated methods for doing so inexpensively (Borker *et al.* 2014, Perkins *et al.* 2017, Hodgson *et al.* 2018). Passive acoustic monitoring is one of the most promising of such methods (Borker *et al.* 2014, Oppel *et al.* 2014). Nevertheless, contrary to expectations we did not find a relationship between acoustic activity and the local nest density around recorders within the colony. This was true using both the number of calls detected by an automated recognition model

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and two acoustic indices (ACI and BIO). Instead GPS tracks of breeding adults intersecting monitoring plots suggests that within-colony flight drives biophony within the soundscape. To our knowledge, this is the first such demonstration of movement patterns driving the biophonic component of a soundscape in an avian species.

We suggest that the lack of a correlation between biophony and local burrow density is robust because several expected patterns were detected in the data. First, acoustic activity was higher during the incubation period, for example, when adults are continuously present within the colony before the chicks become thermally independent relatively early in life (Paiva *et al.* 2010). Additionally, the number of birds in the colony is likely to be highest during incubation before breeding birds fail and leave, and before prospecting males, who are highly vocal, leave the colony (James 1985). Second, the relationships between acoustic activity and environmental variables in our study are consistent with those reported previously (Granadeiro *et al.* 1998, Buxton & Jones 2012, Borker *et al.* 2014). An example of this is the significantly reduced acoustic activity on moonlit nights, a well-known phenomenon thought to be a predator avoidance mechanism (Bretagnolle *et al.* 2000, Oppel *et al.* 2014). We found that acoustic activity declined with wind speed, which we interpret as a reduction in detectability due to associated background noise rather than reduced presence (Buxton & Jones 2012, Oppel *et al.* 2014). Lastly, our findings were consistent across three methods of acoustic analyses, where the only differences observed were in the strength of the relationships. One such difference is the lack of significance in the relationship between the number of calls per hour/night and within-colony flight, likely a result of the species-specific recognition model missing some acoustic activity picked up by the indices. Thus, these well-known patterns, coupled with the consistency of our findings, give confidence in our conclusion that variation in the biophonic component of this colony's soundscape did not reflect within-site variation in the density of breeding birds.

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Several behavioural factors are likely to explain the pattern we observed in our study species. First, it has been suggested that breeding Manx Shearwaters are vocal in flight and quieter on the ground (Perrins *et al.* 1973, James 1985), an effective way of social information transfer without revealing the location of burrows to predators. Immature prospecting birds are thought to be highly vocal in the colony (Perrins *et al.* 1973, James 1985), and thus many of the vocalisations we recorded at sample points were likely a combination of non-breeding birds and breeding birds commuting from elsewhere in the colony. Similarly, as the sexual function to calling early in the season is replaced by calls solely for mate recognition, breeding birds remain quiet through the late incubation and chick-rearing periods (James 1985).

Our findings suggest that breeding birds do vocalise within the colony, albeit away from their own burrow site, is likely explained by social information exchange. Empirical information for social information exchange in seabirds has been proposed in many species to occur at the colonies or on rafts nearby (Birkhead 1985, Burger 1997, Weimerskirch *et al.* 2010, Wakefield *et al.* 2013). While the temporal resolution of our tracking data was too coarse (4 to 12-minute intervals between GPS locations) to identify fine-scale details of these flight paths, the highly consistent distribution of tracks across years suggests that persistent flight paths do occur. The literature suggests that social information exchange is most likely the driver of the consistency in the flight paths observed here, however, it must be noted that other factors such as avoidance of topographical features or olfactory cues may also influence these distributions (Pollonara *et al.* 2015, Yonehara *et al.* 2016). One other possible reason for increased flight through this area is that the west coast of the island faces the Atlantic ocean. Manx Shearwaters are predominantly pelagic in their foraging and are therefore less likely to travel towards the coast of the mainland located to the east of the island. As biotelemetry technology advances, future work could utilise extended battery lives to obtain GPS

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fixes at a finer scale to separate the effects of social information exchange and other factors driving within-colony movement.

The absence of a relationship between the density of birds breeding in the recording plots and acoustic activity suggests, on the one hand, that random sampling of acoustic activity within the breeding colony is not a suitable method for estimating population size through extrapolation in our study colony. On the other hand, given the enormous potential of the method, it remains worth exploring whether passive acoustic monitoring can act as an index of the whole-colony size, for two reasons. First, our data suggests breeding birds were driving the biophonic soundscape and the locations in which they were detected was consistent across years, even if they did not match the exact locations in which they bred. Second, it was notable that the decline in nest density around the recorders as detected by tape-playback across the two years coincided with a drop in acoustic activity. Given the difficulty and time-consuming nature of monitoring many bird populations, coupled with large time intervals between surveys at many sites (as long as 15 years, Mitchell *et al.* 2004), there remains considerable need to fully understand the potential for passive acoustic monitoring in bird populations. We suggest that future studies should examine this across a number of independent sites using cross-year designs, coupled with behavioural tracking to reveal the full potential of this approach.

The authors would like to acknowledge the National Parks and Wildlife service of the Department of Culture, Heritage and the Gaeltacht in Ireland for funding the PhD under the grant code R16331 that made this study possible, and specifically Dr David Tierney for his invaluable support. We thank the BTO special methods committee for the advice on fitting GPS tags. Additionally, the authors would like to thank the owner and boatman of High Island, Feichin Mulkerrin, who accommodated shipping us and the gear to the island. Thank you to the field staff that moved the acoustic recorders and changed batteries when we could not be on the

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island. We acknowledge that this study contains Met Éireann Data licensed under a Creative Commons Attribution-ShareAlike 4.0 International licence. The authors would like to thank Dr Francis Daunt and Dr Fidelma Butler for their helpful comments on the manuscript. Lastly, the authors would like to thank two anonymous reviewers, Dr Lorien Pichegru and Dr Ruedi Nager for their useful comments that greatly improved the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of the article:

Table S1. False negative rates for (i) each plot and (ii) different categories of wind speed (knots) to demonstrate the effect of increased wind on the recording quality and consequently the detection rate of the call recognition model.

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Table 1. Density of apparently occupied burrows (AOB (95% CI)) within a 50 m radius of acoustic recorders across the 12 study plots determined through tape-playback and application of the calculated response rates in 2015 and 2016. The uncertainty around the density estimates reflect the uncertainty around the measured response rates.

Plot	*2015 AOB*	*2016 AOB*	*Average Density AOB*
1	10 (7-13)	7 (5-9)	8.5
2	36 (27-45)	24 (18-30)	30
3	16 (11-21)	11 (8-14)	13.5
4	2 (1-31)	0	1
5	6 (4-8)	2 (1-3)	4
6	16 (11-21)	11 (8-14)	13.5
7	10 (7-13)	6 (4-8)	8
8	2 (1-3)	2 (1-3)	2
9	0	2 (1-3)	1
10	28 (20-36)	18 (14-22)	23
11	2 (1-3)	0	1
12	8 (5-11)	8 (6-10)	8

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Table 2. Model summaries of factors affecting the number of calls detected by the automatic recognition model at both the calls per hour scale (*n* = 850) and calls per night scale (*n* = 170). Effect sizes reported in "log" format as per model outputs.

Factor	*Calls per hour model*			*Calls per night model*		
	Effect	***z***	***P-value***	**Effect**	***z***	***P-value***
Density	-0.02 (± 0.4)	-0.75	0.45	0.01(± 0.02)	0.65	0.52
Incubation	0.36 (± 0.18)	1.96	**0.04**	0.007(± 0.45)	0.01	0.9
23:00-00:00	-0.6 (± 0.18)	-3.42	**< 0.001**	*N.A*	*N.A*	*N.A*
Year: 2016	-2.19 (± 0.2)	-9.11	**< 0.001**	-2.13(± 0.46)	-4.5	**< 0.001**
Moon	-2.41 (± 0.2)	-11.59	**< 0.001**	-2.1 (± 0.4)	-5.13	**< 0.001**
Wind speed	-0.06(±0.016)	-3.82	**< 0.001**	-0.08(± 0.02)	-2.793	**0.005**
Cloud Cover (CC)	0.0336	0.2	0.838	0.473(± 0.3)	1.583	0.114
CC:Moon	0.397	1.94	0.053	-0.553(± 0.4)	-1.48	0.139

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Table 3. Model summaries of factors affecting the biophonic component of the soundscape measured by the Acoustic Complexity Index and the Bioacoustic Index. Effect sizes reported in "log" format as per model outputs.

Factor	*Acoustic Complexity Index (ACI)*			*Bioacoustic Index (BIO)*		
	Effect	***z***	***P-value***	**Effect**	***z***	***P-value***
Density	-0.0002 (± 0.0005)	-0.40	0.68	0.001 (± 0.001)	0.57	0.5
Incubation	0.056 (± 0.01)	3.76	**0.001**	0.28 (± 0.048)	5.72	**0.001**
23:00-00:00	-0.03 (± 0.01)	-2.19	**0.05**	-0.08 (± 0.04)	-2.00	**0.045**
Year: 2016	-0.14 (± 0.1)	-10.44	**0.001**	-0.37 (± 0.05)	-8.04	**0.001**
Moon	-0.4 (± 0.07)	-5.39	**0.001**	-0.97 (± 0.24)	-4.05	**0.001**
Wind speed	-0.004 (± 0.0009)	-5.15	**0.001**	-0.02 (± 0.003)	-8.04	**0.001**
Cloud Cover (CC)	-0.02 (± 0.08)	-2.4	**0.05**	-0.024 (± 0.02)	-0.84	0.4
CC:Moon	0.03 (± 0.01)	3.33	**0.001**	0.068 (± 0.036)	1.9	0.1

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Figures

Figure 1. Map of the study site, High Island, showing the distribution of (a) breeding Manx Shearwaters (apparently occupied burrows (AOB)), (b) nest sites from which GPS tags were deployed and (c) acoustic recording study plots.

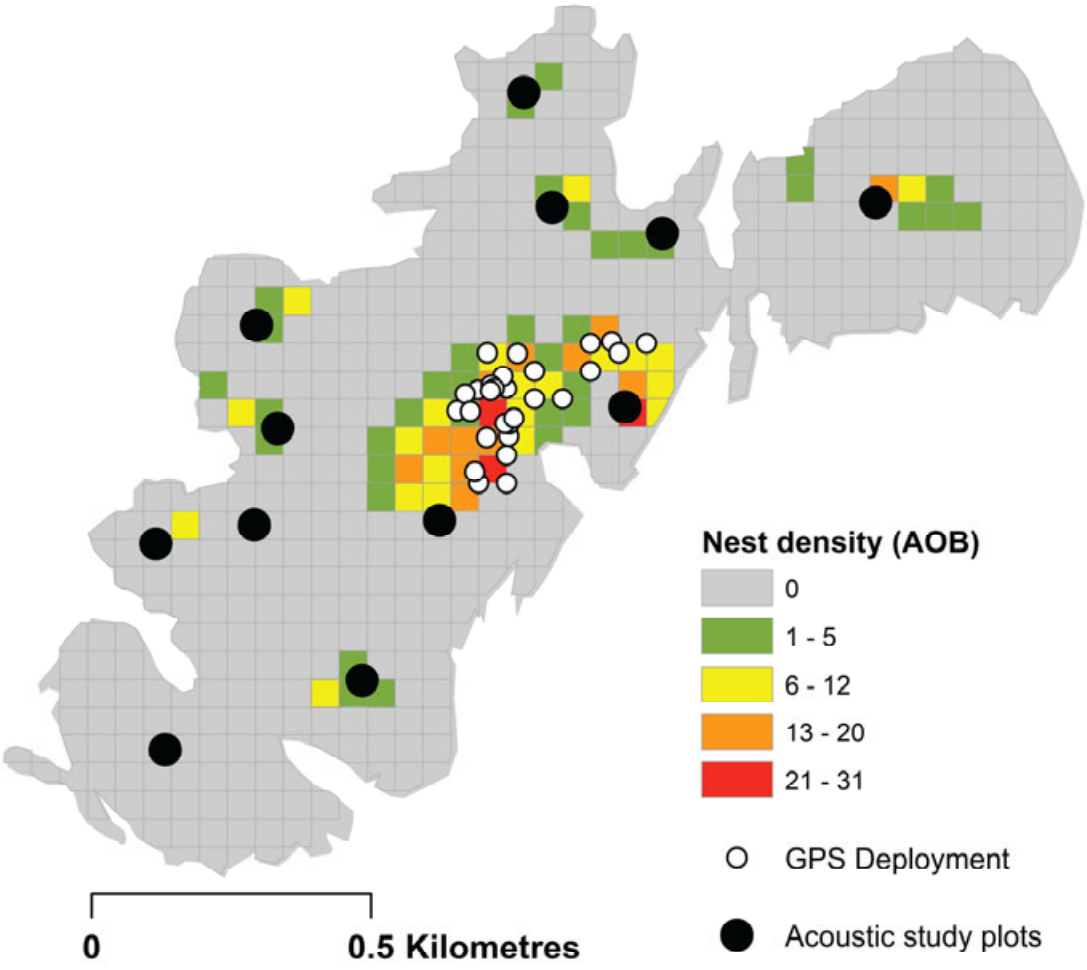
Figure 2. Visualisations of the distribution of (a) the number of flight path intersections by GPS tracked Manx Shearwaters, (b) the mean density of apparently occupied burrows within each study plot, (c) the average number of calls per hour and (d) the average Bioacoustic Index (Boelman *et al*. 2007) as recorded by passive acoustic monitoring.

Figure 3. Scatter plots showing the relationship between average acoustic activity and the mean density of breeding Manx Shearwaters within acoustic study plots on High Island. The top two figures show acoustic activity measured by the number of calls detected by an automated call recognition model at both the hourly and nightly temporal scales. The bottom two figures show the average acoustic activity as measured by the Acoustic Complexity Index (ACI; Pieretti *et al*. 2011) and the Bioacoustic Index (BIO; Boelman *et al.* 2007).

Figure 4. Scatter plots showing the relationship between average acoustic activity and the number of plot intersections by GPS tagged Manx Shearwaters breeding on High Island. The top two figures show acoustic activity measured by the number of calls detected by an automated call recognition model at both the hourly and nightly temporal scales. The bottom two figures show the average acoustic activity as measured by the Acoustic Complexity Index (ACI; Pieretti *et al*. 2011) and the Bioacoustic Index (BIO; Boelman *et al*. 2007).

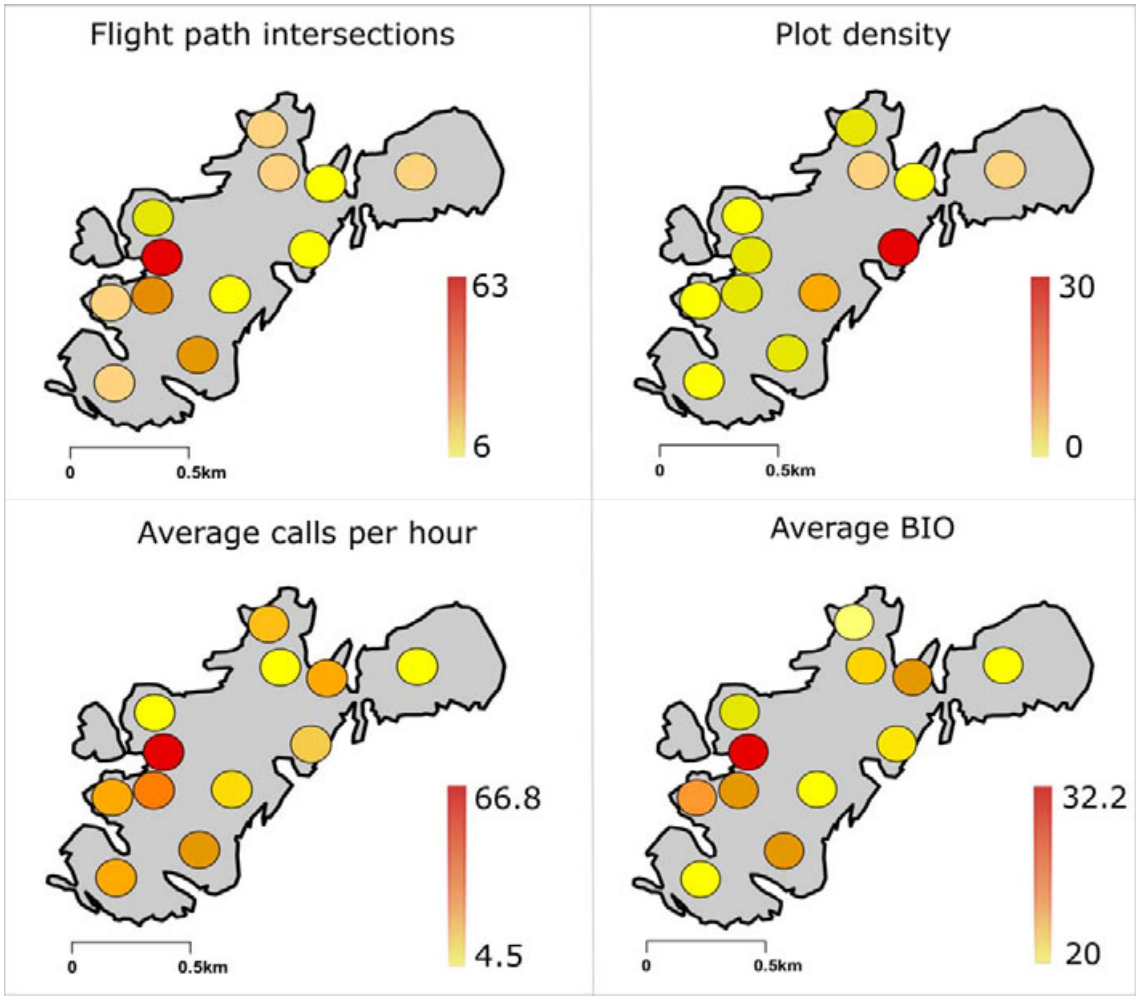
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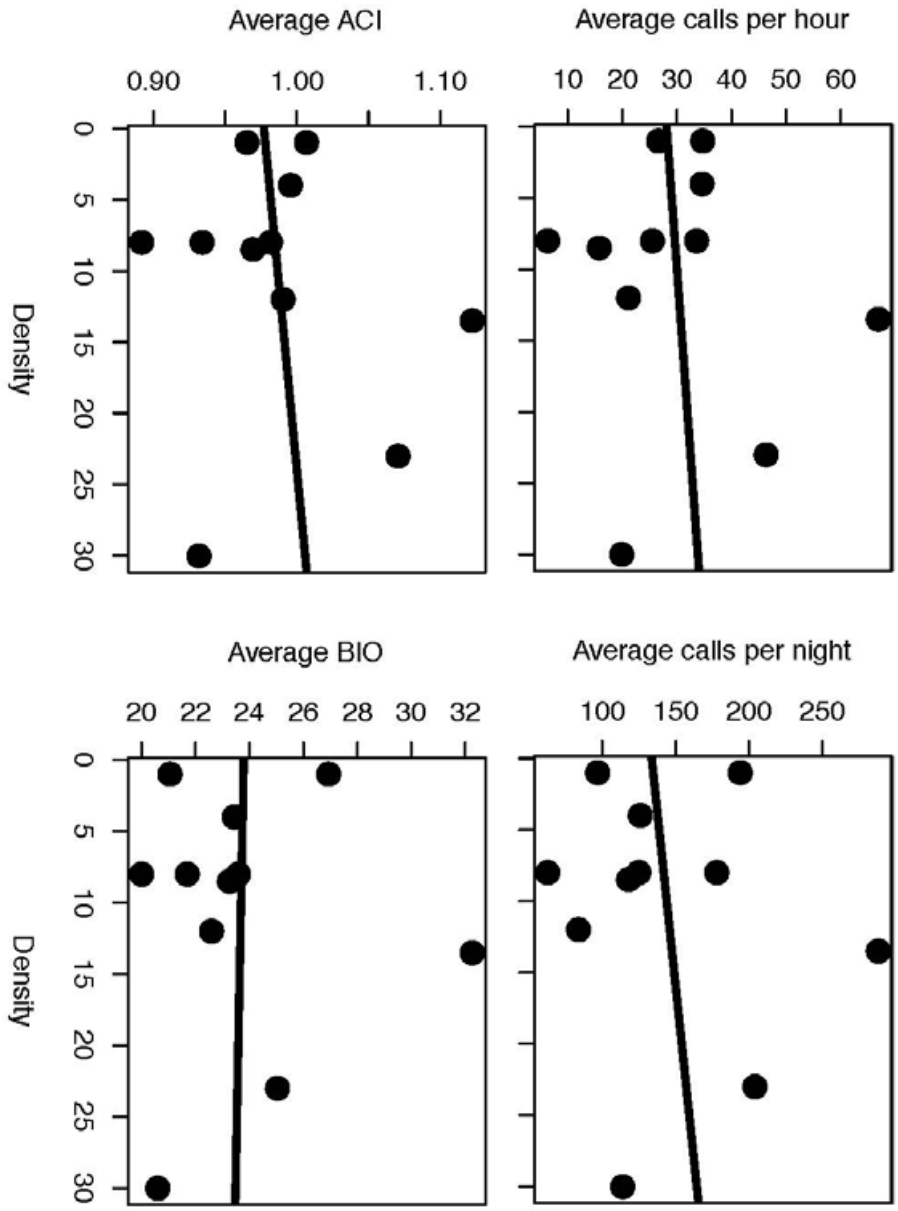
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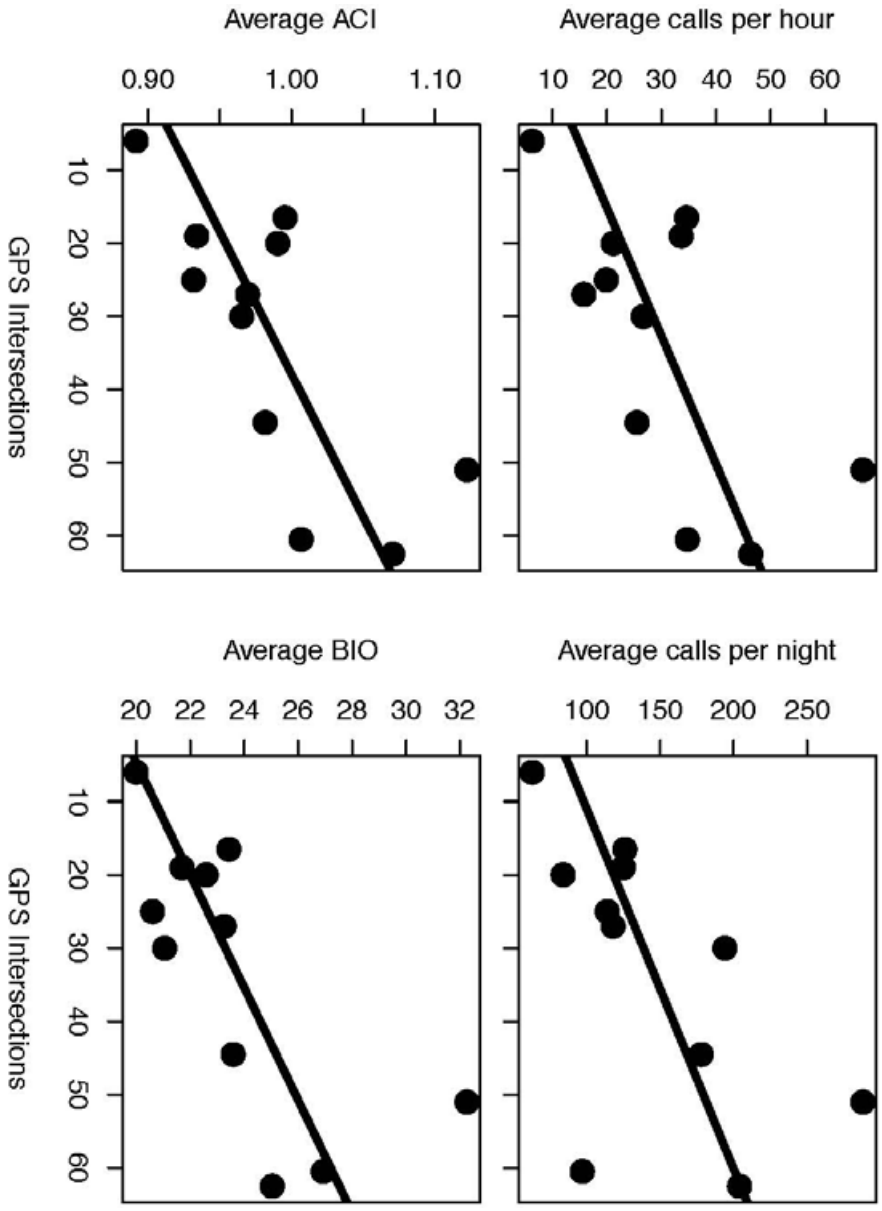
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