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Regional and age-dependent differences in the effect of wind on the migratory routes of Eleonora's falcon

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Abstract During migration, birds can show different responses to wind in relation to distance to the goal, experience, ecological barriers and visibility of landmarks. We analysed the effect of wind (tailwinds and crosswinds) on daily movement rates (forward and perpendicular) of Eleonora's falcons using ARGOS satellite telemetry, during their trans-continental autumn migration to Madagascar, in relation to the different crossed regions and individuals' age class. Our results showed that the effect of wind on daily movement rates was not uniform, being stronger in the farthest region from the migration goal, the Sahara desert, with adults being more affected than juveniles in this region. In the Sahel, the results were more conflicting, perhaps because daily movements were more shaped by the distribution of food resources. In Equatorial Africa, daily movement rates were mainly affected by crosswinds. Still, it remains unclear which orientation mechanism allows Eleonora's falcons to reach such a narrow wintering area compensating also for wind displacement [*Current Zoology* 61 (3): 428–434, 2015].

Keywords Migration, Raptors, Africa, Wind Drift, Satellite Telemetry, Orientation

The movement rate of organisms during migration is determined in large part by the energy they expend. Animals can minimize transport costs by modifying energy expenditure in response to environmental heterogeneity (Shepard et al., 2013). In particular, during migration, animals have to deal with the movement of the fluid in which they actually move, such as birds and insects with winds or fishes with water currents (Chapman et al., 2012). In order to reach their goal, migratory birds must have navigational abilities and need to be able to determine wind direction to cope with wind conditions en route. These abilities can determine the success of the migration and thus of all the other events of the birds' life cycle, since the inability to compensate for wind drift, or the selection of bad wind conditions for departure, can greatly increase mortality risk (Liechti, 2006). Birds show different responses to crosswinds ranging from full drift, to full compensation and even overcompensation (Klaassen et al., 2011). Up to now, the study of these topics has been possible only through tracking radars (Green and Alerstam, 2002; Liechti, 2006) or visual observations (Agostini et al., 2005), limiting general conclusions and restricting analyses to a small portion of the entire migratory route. However, current availability of satellite tracking technologies has enabled the examination of migratory birds along their whole migration routes, allowing the exact identification of final destinations and, consequently, spatially explicit analyses on responses to wind conditions (Thorup et al., 2003, Klaassen et al., 2011). Furthermore, such analyses are also possible thanks to the easier accessibility of large scale meteorological datasets (Kemp et al., 2012). Theoretical and empirical studies on the responses of birds to wind drift allow the identification of the different responses to wind either in relation to the distance to the goal, the landscape characteristics or birds' experience, although these factors have never been analysed simultaneously. In particular, theoretical studies predict that the more distant the goal, the highest the drifting effect, while compensation and overcompensation are expected to occur more frequently closer to the goal (Alerstam, 1979b). Concerning landscape characteristics, birds should be more prone to allow drifting when crossing ecological barriers, areas where environmental conditions are more severe and foraging opportunities are scarcer. Hence, birds would compensate for this drift during the crossing of non-barrier areas to avoid ending in areas distant from their goal areas (Alerstam, 1979*a*, Klaassen et al., 2011). Experience also plays an important role, since adult indi-viduals, being already experienced and able to perform true navigation, should show higher compensation rates than juveniles, which are supposed to be unable to compensate for perpendicular displacement (Drost, 1938, Thorup et al., 2003). Therefore, in order to assess which of these strategies (compensation vs. drift) are acting,

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here we analyse the effect of wind conditions within the same migratory system: the trans-equatorial autumn migration journey of the Eleonora's falcon (*Falco eleonorae*), investigating the effect of wind on forward and perpendicular movements, and accounting for the different passage regions and age-classes. To the best of our knowledge, this is the first analysis of wind drift on a trans-equatorial over-land migrant (in fact only a few papers on seabirds are available in this respect so far, e.g. Felicisimo et al., 2008), and also the first one taking into account both age and regional differences at the same time, while previous papers took into account these aspects separately, e.g. age differences in Honey buzzards (*Pernis apivorus*; Thorup et al., 2003) and regional differences in adult Ospreys (*Pandion haliaetus*) and Marsh harriers (*Circus aeruginosus*; Klaassen et al., 2011). Previous studies on the species reveal that meteorological conditions experienced by Eleonora's falcons along the routes, such as the presence of unfavourable meteorological conditions over the Indian Ocean, promote among-year variability in their migratory tracks (Mellone et al., 2011). In contrast, another study dealing with the whole migration journey during both seasons found no effect of wind conditions upon flight speed (Kassara et al., 2012).

The Eleonora's falcon is a long-distance migratory raptor, which breeds colonially in small islands of the Mediterranean Sea and the Atlantic Ocean (Walter 1979). The wintering range of the species is very small, since almost the whole population concentrates in Madagascar (Walter, 1979). To reach Madagascar, Eleonora's falcons perform a trans-equatorial journey of ca. 10,000 km, flying sometimes also during the nighttime, crossing a huge variety of landscapes, such as deserts, savannahs and forests, with juveniles migrating independently of adults (Gschweng et al., 2008, López-López et al., 2009, 2010, Kassara et al., 2012, Mellone et al., 2013). Therefore, its migration system provides an excellent model to study the regional and age related variation of the response of migratory birds to wind conditions.

1 Materials and Methods

1.1 Migration data

Eleonora's falcons were trapped in Balearic and Columbretes Islands (Spain) in September, between 2007 and 2010 (Fig. 1; details in López-López et al., 2009, 2010, Mellone et al., 2013). Birds were tagged with Microwave Telemetry Inc. 9.5-gram solar-powered satellite transmitters using a Teflon ribbon harness. Transmitters were programmed to collect data on a duty cycle of 12-h ON/15-h OFF during migration. The dataset included 12 individuals (six adults and six juveniles). Two adults were tracked during two consecutive years and hence a total of 14 autumn migration tracks were recorded. Data belonging to the same individuals were considered as independent events, since migrating raptors show high among-year route flexibility (García-Ripollés et al., 2010; Klaassen et al., 2011, Mellone et al., 2011, 2012, Vardanis et al., 2011, Limiñana et al., 2012). In order to identify migration segments, we used locations recorded during the night as start and ending point of these segments (local time: 6 pm-5 am), using only high quality locations (Argos location classes 3, 2, 1 and 0). Eleonora's falcons, in some occasions, migrate also during night (López-López et al., 2010) and hence some nocturnal movements have been included in the segments. However, the large majority of movements within each segment corresponded to day-time migratory movements. Exploratory analyses showed that it was not possible to examine differences in response to winds between day and night because of small sample size and the different temporal resolution of bird location and wind data.

The length of these segments was considered as the daily distance. Since in a few cases night locations were lacking, we also included segments lasting two days (n = 8). In this case, the daily distance was calculated by dividing the segment's length by two (Klaassen et al., 2011). To avoid including data belonging to stopovers,

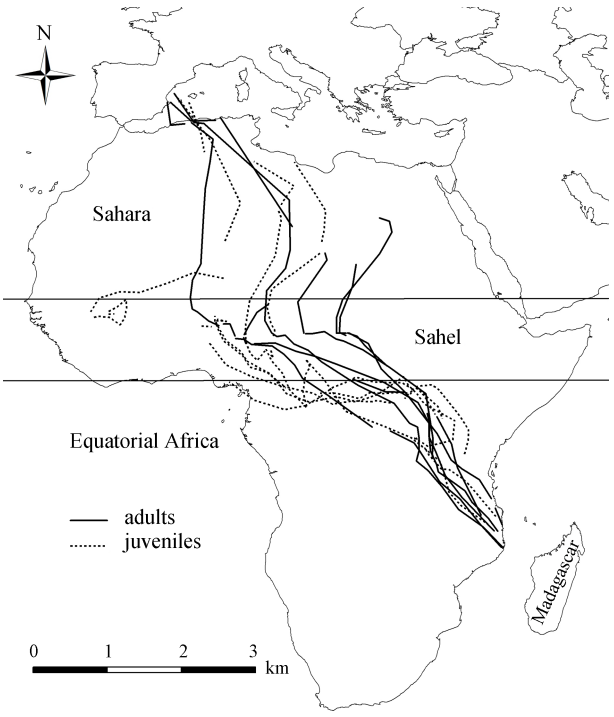


Fig. 1 Autumn migration segments of Eleonora's falcons used for analyses

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segments with daily distance shorter than 75 km were excluded from the analyses (see Klaassen et al., 2011). Every daily segment was assigned to a region (Sahara, Sahel, Equatorial Africa; Figure 1) according to the same criteria used in López-López et al., (2010), though segments South of the Sahel were pooled in a single category since previous studies showed no differences in flight behaviour between the two regions (Equatorial and South-Eastern Africa; López-López et al., 2010).

1.2 Wind data and statistical analyses

Wind data (u and v components of wind vectors) were obtained from the NCEP/NCAR Reanalysis project, as provided by NOAA/OAR/ESRL PSD, Boulder, CO, USA, downloaded through the R package RNCEP (Kemp et al., 2012). Following Klaassen et al. (2011) and Limiñana et al. (2013), we used data from the pressure level of 925 hPa, as this is the altitude at which most of the migration movements of raptors occur (see also Mateos-Rodríguez and Liechti, 2012). To simulate wind conditions experienced by birds in every migration segment we averaged wind data from the beginning (06 h), middle (12 h), and end (18 h) of the segment, giving twice as much weight to the wind conditions in the middle (12 h) of a migration day (Klaassen et al., 2011, Limiñana et al., 2013). Forward and perpendicular components of birds movement (measured as km/day), tailwinds and crosswinds (m/s), were all computed for each migration segment assuming a general migration direction of 135°, which is the direction followed by Eleonora's falcons from breeding colonies to reach Madagascar through the narrowest point of the Mozambique Channel (Gschweng et al., 2008, López-López et al., 2009, 2010, Kassara et al., 2012, Mellone et al., 2013). The effect of wind upon migratory movements was first tested using Generalized Linear Mixed Models (GLMM), in which we fitted the track ID as random factor. Age, wind (tailwind or crosswind) and their interaction were considered as fixed factors, carrying out different models separately for the three regions. Thereby, we carried out six different models for the three regions and for the two dependent variables (forward movement or perpendicular movement), fitting for each case the correspondent wind variable (tailwind or crosswind). Non-significant terms ($P > 0.05$) were removed stepwise from the models according to their P-value within the model, checking before the interactions, until we obtained models that retained only significant variables. Then, we tested the effect of wind by means of linear regression (Thorup et al., 2003, Klaassen et al., 2011, Limiñana et al., 2013), correlating forward components of the migration segments with tailwinds and perpendicular components with crosswinds. Analyses were carried out separately for regional (three) and age (two) categories. Thereby, we computed a total of 12 regressions (i.e., three regions per two age classes per two movement components).

2 Results

Wind conditions had an effect upon movement rates in all regions, albeit results for the Sahel were less marked in comparison with the other two regions (Table 1). Linear regressions were performed for segments shown in Fig. 1 and were significant in eight out of 12 cases, showing that wind affects migratory movements of Eleonora's falcons, although there were large variations among regions (Table 2; Fig. 2). In summary, the stronger effect occurred in the Sahara desert, where both movement components were significantly related to winds in both age classes (Fig. 2). In the Sahel, results were more conflictive, since adults were affected only by crosswinds and juveniles only by tailwinds. In the equatorial region, daily movement rates of both age classes were affected by crosswinds and not affected by tailwinds, although in the latter case the results obtained were almost significant (Table 2).

3 Discussion

We analysed the effect of wind on a trans-equatorial overland migrant across different regions and age clas-

Table 1 Final GLMMs with track (individual) as random factor

	Source	Denominator *df*	*F*	Sig.
Forward component				
Sahara	Tailwind	50.47	28.93	0.001
Sahel*	Age	7.88	5	0.056
Equatorial Africa	Tailwind	135	8	0.005
	Age	135	33.52	0.001
Perpendicular component				
Sahara	Crosswind	48.956	22.606	0.001
Sahel	Crosswind	74.94	14.66	0.001
	Age	8.11	.013	0.912
	Age^x Crosswind	74.94	7.6	0.007
Equatorial Africa	Crosswind	134.44	26.54	0.001
	Age	7.32	12.2	0.009

* in this case no variable was retained in the final model, with "Age" being the last one to be removed; see methods.

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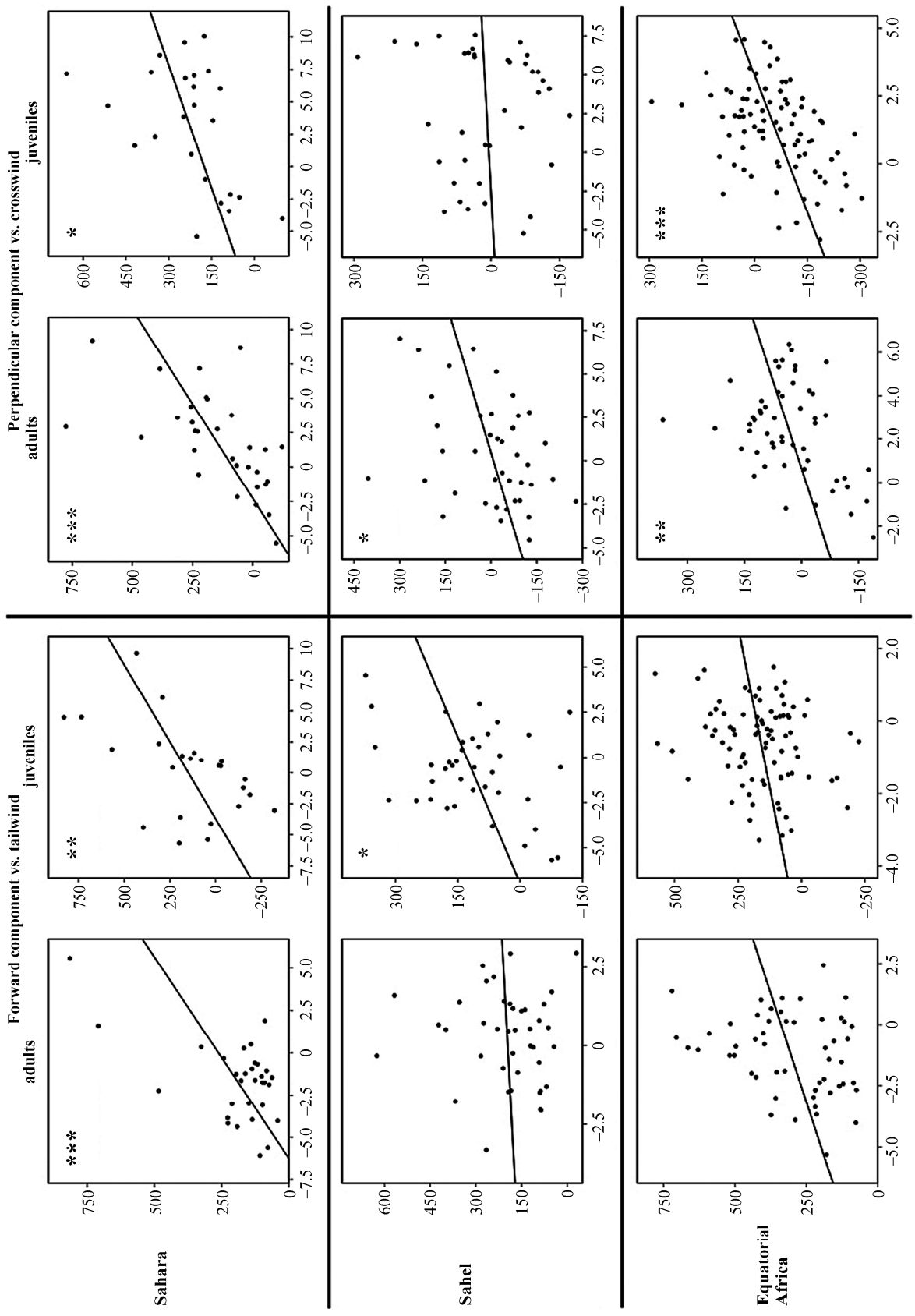


Fig. 2 Scatter plots of rates of movement (km/day) in relation to wind components (m/sec)
Significant results are marked with an asterisk ($P < 0.05$ = *; $P < 0.01$ = **; $P < 0.001$ = ***).

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Table 2 Linear regressions between daily rates of movement (km/day) and wind components (m/sec)

Region	Age	*n*	Forward movement versus tailwind					Perpendicular movement versus crosswind				
			R^2	*P*	Slope	C.I. (95%)	Intercept	R^2	*P*	Slope	C.I. (95%)	Intercept
Sahara	adults	31	0.314	0.001	42.097	18.5–65.7	261.629	0.355	0.0001	36.464	17.8–55.1	82.623
	juveniles	24	0.272	0.009	40.292	11.1–69.5	149.088	0.225	0.019	15.822	2.84–28.8	176.451
Sahel	adults	41	0.003	0.714	5.518	-24.8–35.8	195.358	0.128	0.022	17.094	2.7–31.5	-7.759
	juveniles	38	0.128	0.028	18.53	2.15–34.9	129.218	0.005	0.662	1.851	-6.7–10.4	4.796
Equatorial Africa	adults	53	0.072	0.052	28.091	-0.2–56.4	338.537	0.145	0.005	18.551	5.91–31.2	-11.922
	juveniles	85	0.043	0.056	28.136	-0.8–57.1	176.556	0.19	0.0001	29.758	16.3–43.2	-97.139

Abbreviations: C.I., Confidence interval; ns, non-significant. *P* values of non-significant relationships are given in brackets.

ses. Therefore, overall, the wind effect was higher during the crossing of the Sahara desert, in agreement with theoretical predictions and previous studies, since this region is an ecological barrier and is far from the final goal (Alerstam, 1979a, b). Apparently, in this region the tailwind effect was very strong for both adults and juveniles, and a comparison of the slope values (Table 2) suggested that adults were more affected by crosswinds than juveniles. Considering the restricted wintering range used by the Eleonora's falcon, it may be expected that juveniles have better compensation abilities than shown by Thorup et al. (2003) for the juveniles of other species with wider wintering ranges. However, our observation that adults were fully drifted in this area is striking and deserves further study. Apart from age differences in the Sahara desert, south-western heading segments (thus diverging from the general migration direction) were very frequent (Fig. 1), particularly in the lower third of the region, suggesting that the dog-leg-shaped route of the species may be promoted by wind conditions. The conflicting results obtained for the Sahel region could be accounted for other factors different to winds, as for example birds performing less directed movements in order to search for food resources, particularly juveniles (Gschweng et al., 2008; Kassara et al., 2012; Mellone et al., 2013). In the last region, Equatorial Africa, daily movement rates of both age classes were strongly affected by winds in their perpendicular component, but not in their forward component. This might be explained so as an effort to reach their final goal as soon as possible (i.e., "sprint effect" *sensu* Alerstam, 2006). Thereby, Eleonora's falcons would try to increase daily flight range irrespectively of wind and the effect of wind on instantaneous speed would not be detected at the daily scale.

Concerning the effect of individual experience, GLMMs did not identify an important effect of the interaction between age class and wind conditions across different regions.

A further source of variation in the response to wind could be landmark visibility, which would diminish drastically during nighttime. Hence, the drift effect would be expected to be stronger during nocturnal migration if birds use landmarks to orient, when visual cues are not available (Liechti, 2006; Klaassen et al., 2011). Unfortunately, we could not test this assumption in the present study, although it has been demonstrated that Eleonora's Falcons are able to navigate during both day and nighttime over a featureless landscape like the Indian Ocean (Mellone et al., 2011) exhibiting low levels of repeatability among seasons and years throughout their whole migration route (Gschweng et al., 2008; Kassara et al., 2012; Mellone et al., 2013). Hence, landmark recognition is not likely to be an important cue used by these birds to navigate, as suggested for other long distance migratory raptors such as ospreys, marsh harriers, lesser kestrels *Falco naumanni* and Egyptian vultures *Neophron percnopterus* (Alerstam et al., 2006; Vardanis et al., 2011; Limiñana et al., 2013; López-López et al., 2014).

Overall it seems that Eleonora's falcons migrate more irrespectively of wind conditions than larger soaring raptors (Thorup et al., 2003; Klaassen et al., 2011; Mellone et al., 2012). Similar results have also been obtained with the Lesser Kestrel, a species very similar in morphology and flight mode (Limiñana et al., 2013). This seems to be confirmed also by the low explanatory power of the regressions, especially outside the Sahara desert, where Eleonora's falcons frequently stopped migration probably regardless of wind conditions. However, we cannot exclude that winds affect instantaneous movements more than our analysis is suggesting, although such effect was not visible at the daily scale due to variation in travelling hours among different days or

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because of Argos data accuracy (Safi et al., 2013). Unfortunately, Argos transmitters do not allow computing exactly on a daily basis the number of travelling hours, and earlier analyses suggested a regional variation in this respect (López-López et al., 2010).

Our findings disagree with results of Kassara et al. (2012), which did not find any effect of wind conditions on Eleonora's falcons' migration speed, probably due to the different statistical procedures used, as they classified wind direction only into four categories (thus losing information) and bird speed data was analysed on an hourly scale (maximum 4 hours, thus without matching with spatial/temporal resolution of wind data, as acknowledged also by the authors).

Finally, it still remains a mystery how long-distance migratory raptors such as Eleonora's falcons reach such a restricted wintering area, especially when considering juveniles migrating alone. Certainly, this ability implies that birds not only have a compass sense but they are also able to compensate due to wind drift. It remains an open question whether long-distance migratory birds reaching such narrow goal areas rely only on a map-based orientation system (e.g. according to Earth's magnetic field or celestial cues) or they are able to use any further mechanism (Thorup et al., 2010), like the capability of sensing infrasound radiated from steep-sided topographic features, as suggested by Gschweng et al., (2009; see also Hagstrum 2000, 2013).

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