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On the orientation and homing abilities of wild Rock Doves (*Columba livia livia* Gmelin): a review

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Abstract - The available data on the orientation and homing abilities of wild Rock Doves (*Columba livia livia*) have been reviewed to construct a unified understanding of their spatial behavior. Evidence suggests that these birds use a time-compensated sun compass to select and maintain spatial directions. This ability allows them to rely not only on simple piloting, following landscape features, but also on true navigation mechanisms within their familiar area. Compared to homing pigeons of similar age and flight experience, wild Rock Doves exhibit similar initial orientation but longer return times and greater variability. The initial orientation of wild Rock Doves captured near their colony and released from sites both within and outside their familiar area is rarely homeward-directed, except when food is available near the colony. This suggests that their navigation system is optimized for foraging movements rather than long-distance returns home, as observed in homing pigeons. Further research is needed to investigate other aspects of their navigation mechanisms, such as the possible use of olfactory or magnetic cues. However, genetic introgression with feral and domestic conspecifics poses a significant threat to the conservation of wild populations, limiting opportunities for future studies.

Key words: homing pigeon, homing strategies, initial orientation, foraging flights.

Riassunto - Sulle prestazioni di orientamento ed homing dei colombi selvatici (*Columba livia livia* Gmelin): un riesame.

I dati disponibili sulle capacità di orientamento e homing dei colombi selvatici (*Columba livia livia*) sono stati riesaminati con l'obiettivo di costruire un quadro unitario del loro comportamento spaziale. Le evidenze suggeriscono che questi uccelli utilizzino una bussola solare cronometrica per selezionare e mantenere direzioni spaziali. Questa capacità dovrebbe permettere loro di affidarsi oltre ad un semplice pilotaggio, seguendo le caratteristiche del paesaggio, a un meccanismo di vera navigazione all'interno della loro area familiare. Rispetto a colombi viaggiatori di eguale età e esperienza di volo, i colombi selvatici mostrano un orientamento iniziale simile, ma tempi di ritorno più lunghi associati a una maggiore variabilità. L'orientamento iniziale di colombi selvatici catturati nei pressi della colonia e rilasciati da siti entro e fuori dalla loro area familiare raramente è diretto verso casa, a meno che non vi sia cibo disponibile nelle vicinanze della colonia. Ciò suggerisce che il sistema di navigazione dei colombi selvatici sia adattato a ottimizzare gli spostamenti per il foraggiamento piuttosto che a governare lunghi voli di ritorno verso casa, come osservato nei colombi viaggiatori. Ulteriori ricerche sarebbero necessarie per esplorare altri aspetti del loro meccanismo di navigazione, ma l'introgressione con razze domestiche rappresenta oggi una minaccia alla conservazione delle popolazioni selvatiche, limitando le opportunità per future ricerche su di esse.

Parole chiave: colombo viaggiatore, strategie di homing, orientamento iniziale, voli di foraggiamento.

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INTRODUCTION

The late German zoologist Gustav Kramer, one of the outstanding students of bird orientation, expressed the intention of establishing a captive group of wild Rock Doves (hereafter Rock Dove) with the aim of studying their orientation (Kramer & von St. Paul, 1950). The interest in studying this wild species stemmed from the fact that both homing pigeons and other breeds of domestic pigeons, as well as feral pigeons, are descendants of this ancestral species (Darwin, 1868; Goodwin, 1970; Johnston & Janiga, 1995). The homing pigeon is a domestic breed specifically selected for its ability to quickly return to its home aviary. This unique characteristic has made it the preferred model organism for studying the mechanisms underlying avian homing behavior (Wallraff, 2005). It is widely recognized that knowledge of the natural history of model organisms enhances their utility as research models (Alfred & Baldwin, 2015). As a consequence, the question can be posed whether the orientation capabilities of homing pigeons are an extension of qualities inherent in their wild ancestor. Tragically, Kramer died in southern Italy (Calabria region, near the town of Civita) while attempting to reach a nest of Rock Doves, so his objective remained unfulfilled until 1975 when Alleva *et al.* published the first experiments comparing the homing behavior of Rock Doves with that of homing pigeons of the same age and flight experience. These authors, as Kramer had envisioned, worked with two groups of individuals, descended from Rock Doves trapped on the island of Sardinia and central Italy (Abruzzi region), then raised near Pisa and in Rome, respectively (Alleva *et al.*, 1975; Visalberghi *et al.*, 1978).

Further experiments on the initial orientation behavior of Rock Doves were carried out using a completely different method, by singly releasing birds trapped at their colonies and later displaced at different distances (Baldaccini *et al*., 1988; Baldaccini *et al*., 2001; Giunchi *et al*., 2003). The colonies were the same from which the parental individuals transported to Pisa were taken, located along the rocky cliffs of Capo Caccia, from Cala dell'Inferno to Punta Cristallo (Nurra di Alghero, Sassari).

This review discusses the data from the above-cited papers, which remain the only ones present in the ornithological literature, with the aim of providing a comprehensive picture of the orientation mechanisms used by Rock Doves, their behavioral responses when displaced from their home aviary or colonial sites, and a direct comparison of their homing abilities versus those of homing pigeons. The review is prefaced by some field observations of the daily foraging flights performed by the Rock Doves at their Sardinian colonies (Baldaccini *et al*., 2000), noting that the navigation capabilities of pigeons should be linked to the way in which the wild birds move.

FIELD OBSERVATIONS AT CAPO CACCIA COLONIAL SITE

As suggested by the name, the preferred nesting habitats of Rock Doves are rocky cliffs, both inland and along lakes and seashores (Goodwin, 1970). Being a granivorous species, finding food in the proximity of such habitats can be challenging. Therefore, they have to fly far from their colonial sites in search of feeding grounds. One of the most remarkable aspects of their spatial behavior is the "fast commuting flights" (Goodwin, 1970), i.e., the daily foraging flights to and from the feeding patches. At their colonial sites of Capo Caccia, these flights had two peaks (early morning and afternoon) from March to November, while in the other months, the displacements occurred with a single peak around noon, as reported by Baldaccini *et al.* (2000).

At the time of our observations, the birds of Capo Caccia left their nests shortly after sunrise and usually gathered in sometimes large flocks (up to 250 individuals) on the summit of the rocky cliffs. These flocks then took off for foraging at staggered intervals, departing from the colonies one after another. Fig. 1 shows the east-northeast course

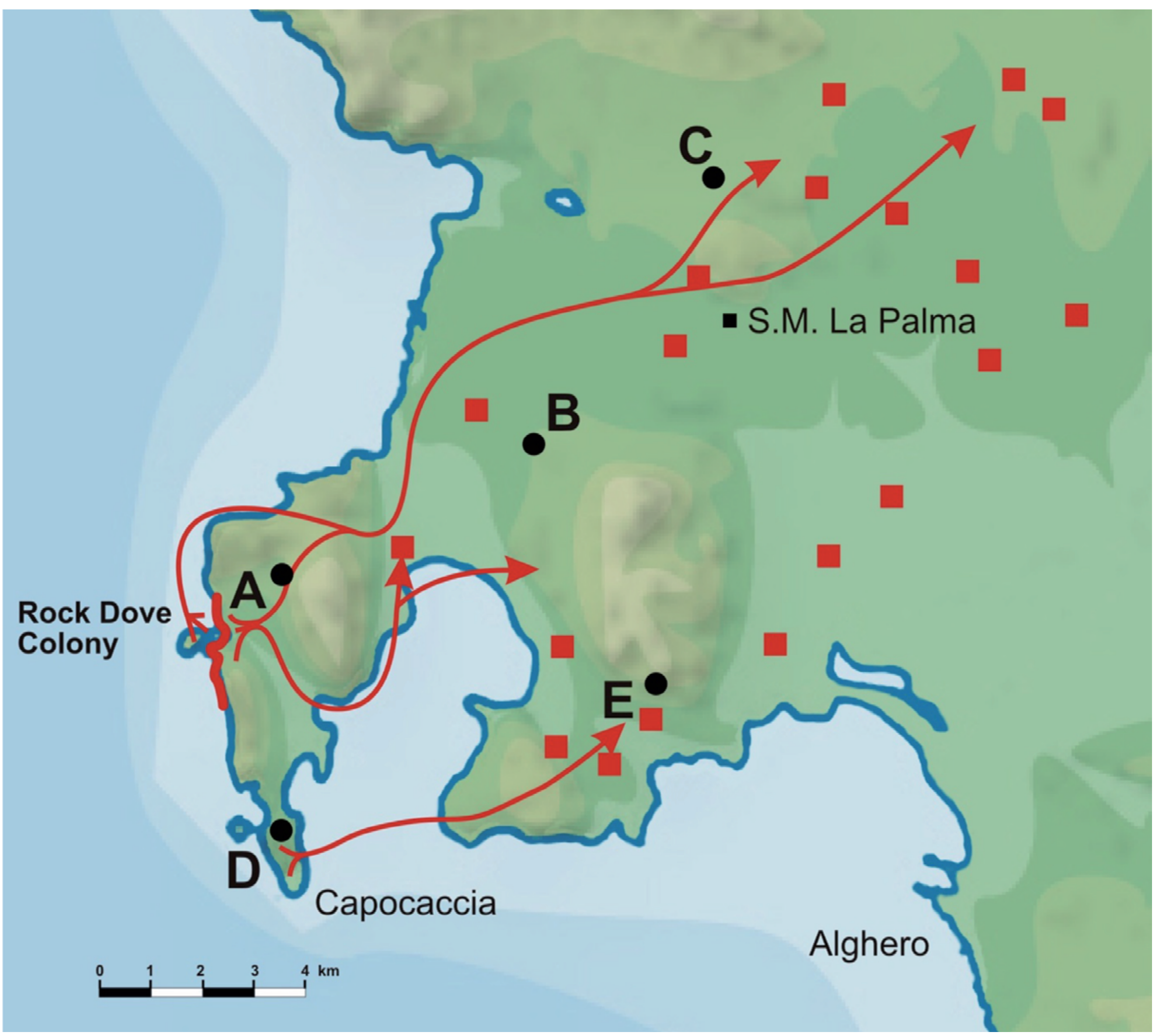

Fig. 1 – Map of the Capo Caccia area showing the location of the Rock Dove colony (highlighted in red along the coastal cliff), observation points (A-E), main foraging routes (arrows), and feeding sites (red squares). / Mappa dell'area di Capo Caccia che mostra la localizzazione della colonia dei Colombi selvatici (linea rossa ispessita lungo la falesia costiera), i punti di osservazione dei movimenti di foraggiamento (A-E), le loro principali rotte (frecce) e la localizzazione dei luoghi di foraggiamento (quadrati rossi).

usually followed in these commuting flights, which remained stable over long periods as revealed by observations in different seasons and years (Baldaccini *et al.*, 1988; Baldaccini *et al.*, 2000).

In particular, the route passing points A to C in Fig. 1 seems to be the most traditional, based on observations dating back as far as 1971 (Alleva *et al.*, 1975). The Rock Doves reached locations situated at distances of between 4 and 26 km, feeding on pastures, arable fields, vineyards, cereal stubble, and Mediterranean scrub. The return journeys to the colonial sites followed a temporal distribution similar to that of the departing flights, with a phase shift of two to three hours. The birds returned individually or in small flocks of several pigeons (see Baldaccini *et al*., 2000, bearing in mind that all the data regarding foraging routes, feeding site locations, and spatial behavior have been recorded visually without any tracking devices).

The almost total cessation of the commuting flights had often been observed in November, when the fruits of lentiscus (*Pistacea lentiscus*) ripened just at the border of the cliffs where the birds had their nests. Flowering and ripening of lentiscus did not occur every year, but when fruits were present, the birds remained within a few hundred meters of their colonies, feeding all day long in groups perched on the *Pistacea* bushes, and watering in some large puddles present in that autumn period in the nearby surroundings.

The range of distances over which the feeding flocks were observed likely represents the extent of the birds' daily radial flights from the colonies at Capo Caccia, providing an approximate idea of their familiar area. However, we cannot rule out that this area might be underestimated, as no tracking devices were used to monitor the foraging flocks, as noted above.

Wild Rock Doves have a sun compass

Birds have an advanced compass sense based on celestial and geomagnetic cues to select and maintain an intended spatial course (Hansson & Åkesson, 2014; Durieux & Liedvogel, 2020). Even within the home range, landmark recognition seems to be integrated within a compass frame; hence, a compass plays an important role for homing pigeons' orientation also over very familiar areas (Graue, 1963; Fuller *et al*., 1983; Biro *et al*., 2007). The homing pigeon is known to have a sun and a magnetic compass (Keeton, 1971; Schmidt-Koenig, 1990), but no experiments have ever been made to provide evidence of a magnetic compass in the Rock Dove, nor on other breeds of domestic or feral pigeons. On the contrary, it has been demonstrated that the Rock Dove possesses a sun compass (Baldaccini *et al*., 2001; Giunchi *et al*., 2003).

Among the different methods to demonstrate the use of a time-compensated sun compass in a given species, the shift of the internal clock produces reliable, predictable, and unequivocally interpretable results in homing pigeons (Schmidt-Koenig, 1990). Thus, clock shift has been widely used as an experimental tool, and it produces a deflection of birds' initial orientation when they are displaced at different distances from home or even when the goal was plainly visible to the human eye from the release site (Schmidt-Koenig, 1990; Armstrong *et al.*, 2013).

In Baldaccini *et al.* (2001), a group of experimental Rock Doves from the Capo Caccia colony was subjected for more than 6 days to a fast-shifted artificial photoperiod of 6 hours and 40 minutes, meaning that their internal clocks were advanced by this amount of time. This shift is expected to produce a counter-clockwise mean deflection in the heading of the experimental birds by approximately 107° relative to the mean heading of the control birds, subjected in an open aviary to a natural photoperiod for the same amount of time. In two releases performed inside their familiar area, the deflection achieved was very close to the expected one [105° and 95°, respectively (Fig. 2A and B)]. In Giunchi *et al.* (2003), the Doves were instead slow-shifted by 5 hours 45 minutes, from which a mean clock wise deflection of 92° was expected. When released from the same site as before, their mean deflection was still as predicted, even if smaller than expected (55°; Fig. 2C).

These tests indicate that Rock Doves use a time-compensated sun compass mechanism to orient their movements. This behavioral trait has thus been preserved in the domesticated homing pigeons. It is interesting to note that, according to Chelazzi and Pineschi (1974) and Edrich and Keeton (1977), feral pigeons can also use a time-compensated sun compass. It is worth noting that feral pigeons exhibit high genetic variability across different populations, largely due to the presence of various domestic pigeon breeds, including the homing ones, within their gene pool (Giunchi *et al*., 2020).

The homing behavior of Rock Doves

Test releases with wild birds bred in aviaries

The aim of these tests was to realize a direct comparison between the homing performances of Rock Doves and those of homing pigeons. To this end, the birds trapped in the Sardinia and Abruzzo regions were housed in aviaries located in the field station of Arnino near Pisa (Ar birds) and in a large terrace in the center of Rome (Ro birds), respectively. In both localities, their descendants were transferred when fledglings to a neighboring aviary, where a comparable number of homing pigeons of the same age were also housed in a separate part of the same loft. Thus, the birds were exposed to the same environmental stimuli.

First group of experimental releases

The experimental displacements took place in 1974 and 1975 with 1- or 2-year-old birds. Before testing, the Rock Doves and homing pigeons were trained separately in flock releases at distances from 0.7 to 10 km. No birds were lost during these training flights. For the experimental tests, the birds were differently released in directional and non-directional series up to 44.5 km (Ar birds) and 75.5 km (Ro birds).

When released individually, only 4 out of the 23 Rock Doves left the release area, while the rest landed nearby, attracting other released birds. By contrast, only 4 out of the 24 homing pigeons landed or disappeared behind the vegetation.

In group releases, the Rock Doves showed a lesser tendency to land, doing so in only two out of eight trials, while all (n=9) the homing pigeon flocks vanished, resulting in mean homeward oriented, as shown in Fig. 3. At all tested distances, the Rock Doves performed worse than the homing pigeons in both individual and group releases; however, the study did not statistically analyze the homing data. At a distance of up to 10 km, no birds were lost, but at 15-20 km, evident differences emerged, with the Rock Doves that always homed the day after release, while the homing pigeons returned within the same day. At greater distances (up to 75.5 km), some Rock Doves began to get lost.

<u>Second group of experimental releases</u>

Two additional series of experimental releases were published 3 years later by the same authors.

The Rock Doves used in these experiments were all bred in the Arnino aviary. The group included some experienced birds that successfully homed in previous experiments by Alleva *et al.* (1975), as well as their offspring, less than one year old, being tested for the first time. Consequently, the possibility of a selective effect, where birds that were more skilled at navigation or more motivated to home were over-represented, cannot be ruled out. In these tests, all birds were individually released, and unlike the previous experiments, their tendency to land upon release was not noticeable. In particular, there was no difference in this respect compared to the behavior of the homing pigeons.

In the 1976 series of experiments, 13 Rock Doves and 13 homing pigeons were released from four sites at increasing distances (6.3 to 30.8 km) southeast of the home loft (directional series). Both groups showed significant orientation towards home, but the homing pigeons were faster in 21 out of 26 pairs, all returning to the loft, while three Rock Doves did not.

In the 1977 series of experiments, 18 Rock Doves and 18 homing pigeons were released from seven sites between 6.5 and 93.5 km from the home loft in various directions (non-directional series). The Rock Doves groups showed significant homeward orientation as the homing pigeons in six out of seven releases (Fig. 4) (Visalberghi *et al.*, 1978),

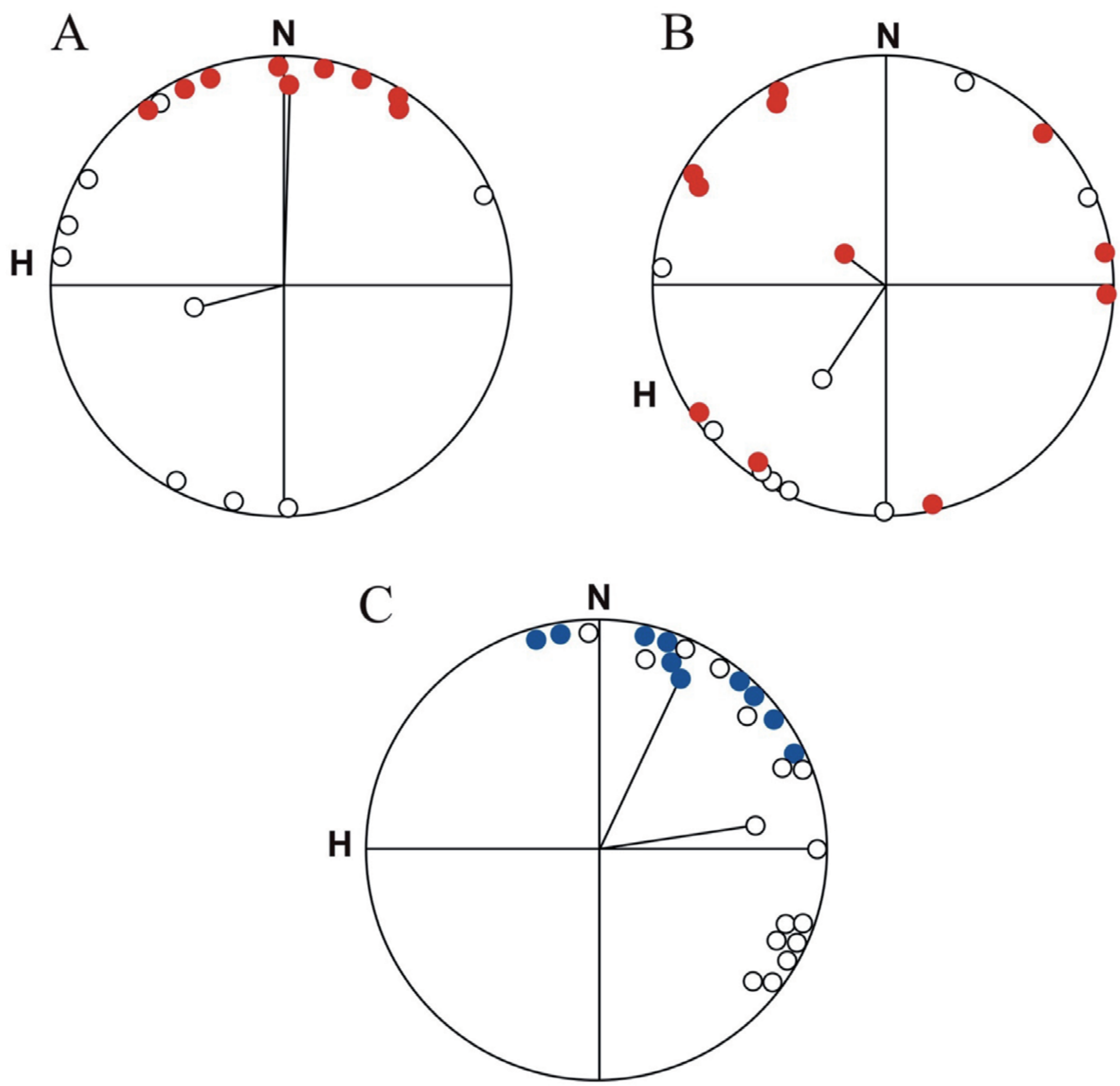

Fig. 2 – Vanishing diagrams from the clock-shift experiments with Rock Doves released within their Capo Caccia familiar area. Filled symbols indicate control birds; open symbols refer to fast-shifted individuals in panels A–B, and slow-shifted ones in panel C (radius=1). The results demonstrate the use by wild Rock Doves of a sun-compass to determine their departure direction. / Diagramma di svanimento dei Colombi selvatici di Capo Caccia soggetti a modifica dell'ora soggettiva in esperimenti di rilascio entro la loro area familiare. Simboli pieni per i colombi di controllo; quelli vuoti si riferiscono in A-B ad individui con ora soggettiva anticipata, in C quelli con ora ritardata (raggio del diagramma=1). I risultati dimostrano l'uso di una bussola solare cronometrica nello scegliere la direzione di involo.

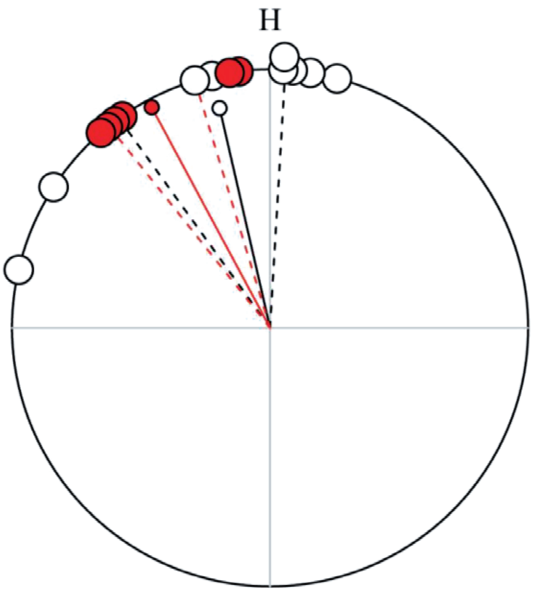

Fig. 3 – Vanishing bearing distribution of flocks of homing pigeons (open symbols) and Rock Doves (red symbols) performed in 1975, with respect to the home direction (H) set to 0° (radius=1). Mean vectors (small symbols) and 95% confidence intervals (dashed lines) calculated using bootstrap with 9999 iterations are also reported. Data from: Alleva *et al*., 1975. / Distribuzioni dei punti di svanimento dei gruppi di colombi viaggiatori (simboli vuoti) e di Colombi selvatici (simboli rossi) rilasciati nel 1975, rispetto alla direzione di casa (H) posta a 0° (raggio del diagramma=1). I simboli più piccoli rappresentano i rispettivi vettori medi con i relativi intervalli di confidenza al 95% (linee tratteggiate) calcolati mediante bootstrap con 9999 iterazioni. Dati da Alleva *et al.* 1975.

but the Rock Doves homed consistently slower than the homing pigeons in 58 out of 63 pairs. Additionally, nine of the 12 Rock Doves in their first year of flight experience were lost during the first three releases, at distances of 6.5, 10.8, and 21.8 km from the home loft. No homing pigeons of the same age were lost in any of the tests.

Overall, the experiments by Alleva *et al*. (1975) and Visalberghi *et al*. (1978) demonstrate that Rock Doves bred in aviaries, when given initial non-directional training releases within a 10 km radius (i.e., the same treatment young homing pigeons receive at the beginning of their flight training), can exhibit homing behavior comparable to that of homing pigeons for displacements up to 30–40 km and for directional releases. However, at greater distances, especially up to 90 km, the performance of Rock Doves declines significantly, with higher loss rates. Despite similar homeward orientation between Rock Doves and homing pigeons, the Rock Doves showed greater variability in their vanishing bearings.

Additionally, they displayed a noticeable tendency to land upon release in the Alleva *et al*. (1975) study, attributed to handling stress. In fact, even if accustomed to their breeder, the Rock Doves "behaved very timidly, were frightened", and some were very difficult to capture before the release tests. To avoid these stressful moments, in the Visalberghi tests, the Rocks "were always caught before dawn and left inside baskets until after sunrise". Then they were transported to the release site, where they remained uncovered for at least 30 minutes before being released. Ultimately, the Rock's homing performance was consistently

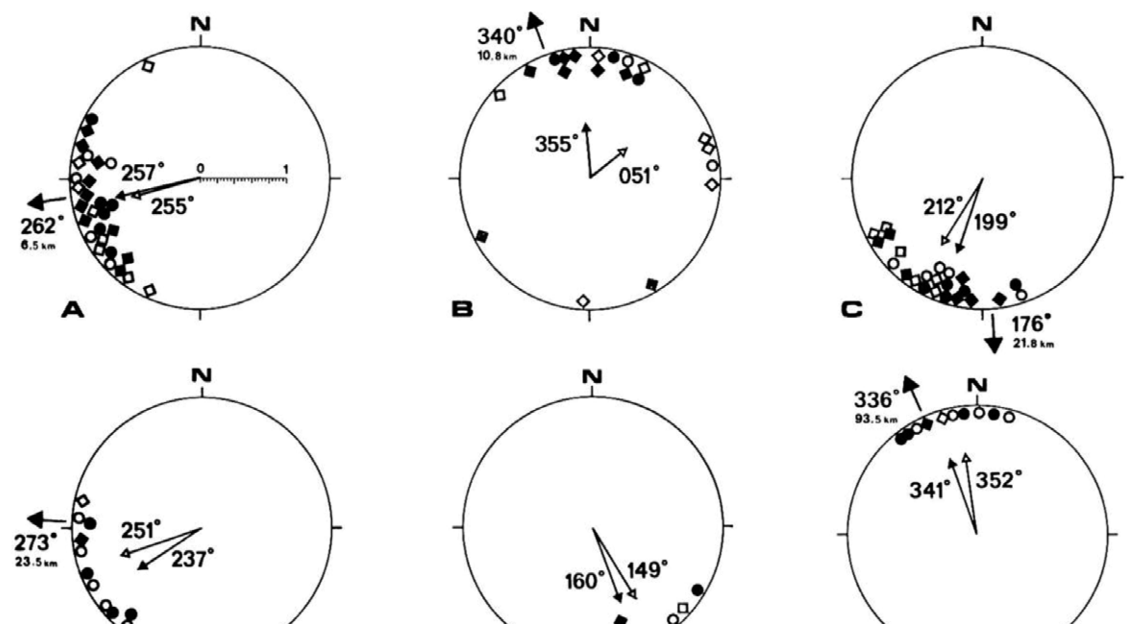

Fig. 4 – Vanishing diagrams for Rock Doves (open symbols) and homing pigeons (filled symbols) in the non-directional series performed in 1977. Bearings of experienced birds are shown as circles, those for juveniles as squares. The direction and distance from home are indicated by the outer arrow. The mean vectors are represented by inner arrows, whose length can be read on the scale given in the first diagram. Modified from: Visalberghi *et al.*, 1978. / Diagrammi di svanimento dei Colombi selvatici (simboli vuoti) e dei colombi viaggiatori (simboli pieni) nella serie di rilasci non direzionali eseguiti nel 1977. I punti di svanimento degli individui con esperienza pregressa di homing sono rappresentati con cerchi, quelli al primo rilascio con quadrati. La freccia esterna indica la direzione e la distanza dalla colombaia. Le frecce interne indicano la direzione di svanimento media per ciascun gruppo, la cui lunghezza può essere letta sulla scala (0-1) riportata nel primo diagramma. Figura tratta da Vialberghi *et al.* 1978, modificata.

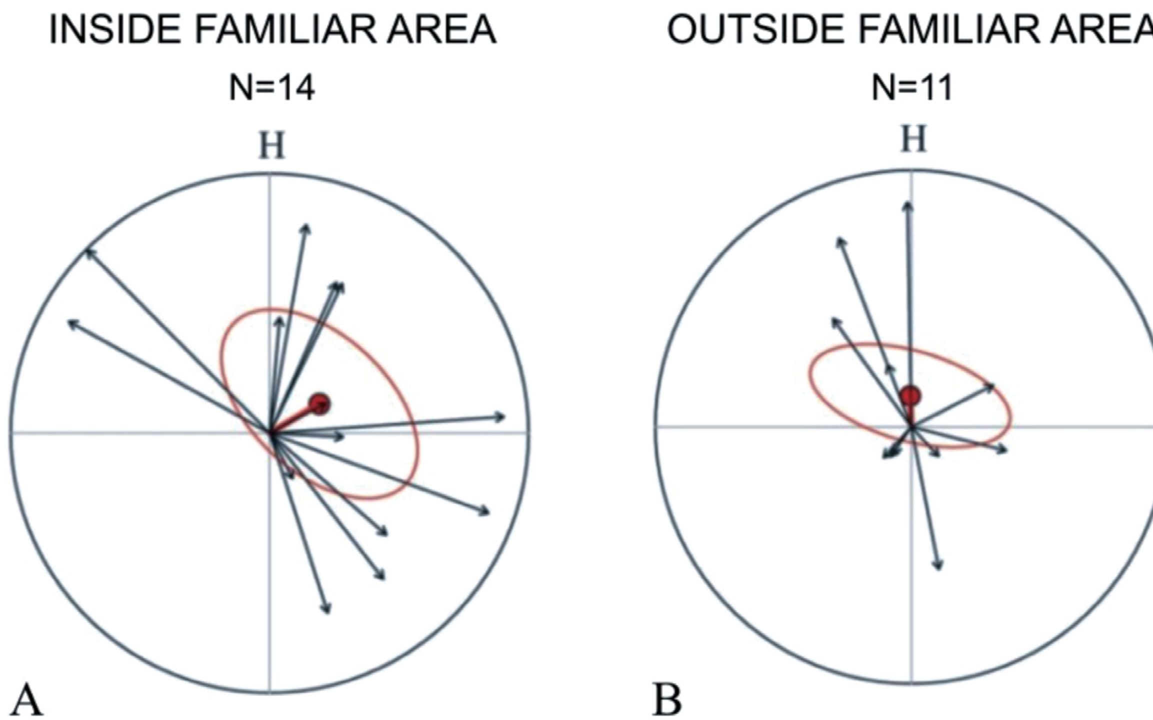

Fig. 5 – Mean vector distributions of test releases performed with Rock Doves inside (A) or outside (B) their familiar area, pooled with respect to the home direction (H) set at 0° (radius=1). The second-order mean vector and the associated 95% confidence ellipse are shown in red. The value of the one-sample Hotelling T^2 test is 5.80, P=0.11 for the A distribution, and 1.06, P=0.64 for the B distribution. Data from: Baldaccini *et al*., 2001; Giunchi *et al*., 2003. / Distribuzioni dei vettori medi dei singoli rilasci eseguiti con Colombi selvatici entro (A) o fuori (B) dalla loro area familiare, cumulati rispetto alla direzione di casa (H) posta a 0° (raggio del diagramma=1). Il vettore medio di secondo ordine e la relativa ellisse di confidenza al 95% sono indicati in rosso. Il valore del test di Hotelling T^2 a un campione è di 5.80, P=0.11 per la distribuzione A; di 1.06, P=0.64 per la B. Dati da Baldaccini *et al.* 2001; Giunchi *et al.* 2003.

worse than that of the homing pigeons across most tests, except in one release by Visalberghi *et al.* (1978), where no significant differences were observed.

Experiment in Sardinia with mist-netted Rock Doves

The main difference between these tests and those reported above is that, in this case, the Rock Doves were mist-netted near point A in Fig. 1 early in the morning, at the very beginning of their daily foraging flights. They were ringed and then displaced to the release site during the same morning. Additionally, a different group of Rock Doves was used for each test. The aim of these tests was to determine whether the Rock Doves were homeward oriented when displaced within their presumed familiar area, as estimated by Baldaccini *et al*. (2001), or from supposed unfamiliar sites.

From 1987 to 2001, a total of 14 test releases were conducted within the familiar area (16.4-19.8 km from the home colony) and 11 tests from unfamiliar sites (29.4-103.2 km). In total, 186 birds (with 108 recorded vanishing bearings) were released within the familiar area, and 181 (with 108 recorded bearings) from outside it. The second-order analysis of the mean vectors of these releases suggests that in both familiar and unfamiliar areas, the Rock Doves did not head toward home upon release (Fig. 5).

However, tests performed within the familiar area in November, when foraging flights nearly cease due to the ripening of lentiscus fruits near the colony, showed significant homeward orientation (Fig. 6). For these autumn releases, the Rock Doves were trapped using mist-nets positioned in

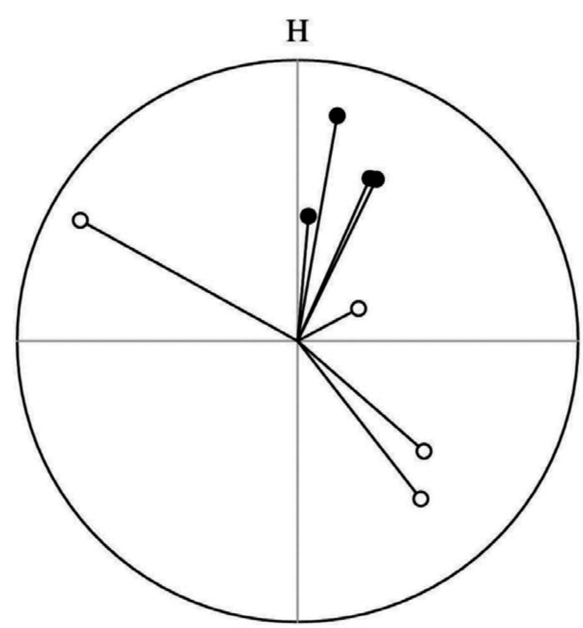

Fig. 6 – Mean vector distribution of test releases performed with Rock Doves from the same familiar sites during April-October (open symbols) or in November (black symbols) in the period 1987-1997, with respect to the home direction (H) set to 0° (radius=1). Data from: Baldaccini *et al*., 2001. / Distribuzione dei vettori medi di rilasci di Colombo selvatico dallo stesso sito in area familiare in Aprile-Maggio (simboli vuoti) ed in Novembre (simboli pieni) nel periodo 1987–1997, rispetto alla direzione di casa (H) posta a 0° (raggio del diagramma=1). Dati da Baldaccini *et al.* 2001.

the lentiscus bushes at the top of their nesting cliffs and near some watering puddles. The homeward orientation recorded only in November, when feeding sites were located close to the home colony, suggests that the initial orientation of displaced Rock Doves was mainly driven by their motivation to reach feeding sites. In November, with feeding sites near home, the Rock Doves exhibited homeward orientation. In contrast, during the spring-summer period, when foraging areas were farther from the home colony, the birds showed no significant tendency to head toward home.

If this explanation is correct, it might be suggested that Rock Doves at least have a detailed knowledge of their familiar area, where they can use familiar landmarks to optimize their spatial behavior in terms of anti-predatory and foraging strategies.

CONCLUSIONS

The experiments reviewed here provide key insights into the homing mechanisms and performance of Rock Doves.

Rock Doves possess a solar compass, which they use to select and maintain a specific spatial course. Studies on homing pigeons have extensively documented the role of visual cues in homing from familiar areas, within two distinct navigational strategies (Filannino *et al*., 2014; Guilford *et al*., 2014): a site-specific compass orientation strategy and a piloting strategy. In the site-specific compass orientation strategy, pigeons use a "mosaic map" (sensu Wallraff, 1974), a mental representation of landmarks and their spatial relationships, encoded as compass directions. The piloting strategy, on the other hand, involves following chains of visual landmarks, largely independent of the solar compass. While direct evidence of Rock Doves using visual landmarks is limited, it is likely that their solar compass aids in developing a directionally oriented mosaic map. This inference is supported by the fact that clock-shifted pigeons predictably alter their heading when released within their familiar area (Baldaccini *et al*., 2001; Giunchi *et al*., 2003). Although it is challenging to define the exact extent of this map, since it depends on the range of individual exploratory flights (Wiltschko & Wiltschko, 1982; Wallraff *et al*., 1994), its size likely corresponds to the typical range of Rock Doves' foraging flights.

Rock Doves demonstrate the ability to return home from unfamiliar locations within a radius of at least 90 km from their home aviary, provided they are non-directionally trained with short-distance releases of increasing distance. Trained Rock Doves exhibit orientation accuracy comparable to that of homing pigeons of the same age and flight experience (Alleva *et al*., 1975; Visalberghi *et al*., 1978). However, their re-entry behavior is significantly inferior to that of homing pigeons, both in return times and the number of individuals lost, highlighting key differences in homing efficiency between wild and domesticated pigeons (Visalberghi *et al*., 1978).

This disparity suggests that selective breeding has enhanced the homing abilities of homing pigeons, making them more efficient homers. The superior homing performance of homing pigeons compared to Rock Doves is expected. As noted by Levi (1974), homing pigeons have been selectively bred for faster returns, resulting in notable morphological and behavioral adaptations. Modern homing pigeons possess greater muscle mass and a stronger homing drive than Rock Doves, contributing to their superior homing skills.

Edrich and Keeton (1971) suggested that feral pigeons are more socially- or flock-oriented than homing pigeons, and Goodwin (1981) similarly described Rock Doves as more flock-oriented than feral pigeons. It is speculated that Rock Doves have a greater tendency to join flocks of other pigeons they encounter during homing flights, which may partially explain their slower return times and generally lower rates of return.

The results from the tests in Sardinia, where Rock Doves exhibited weak homeward orientation except when lentiscus fruits ripened near their home colonies (Baldaccini *et al.*, 2001), further suggest that Rock Doves rely on an orientation and navigation system optimized for short-distance commuting within the familiar area, rather than the strong long-distance homing drive typical of homing pigeons.

While it seems reasonable to assume that Rock Doves use visual landmarks for homing, there is insufficient information as to whether they employ additional cues. Homing pigeons are known to rely on multiple cues (Semm & Beason, 1990), including olfactory ones, with odorous substances carried by the wind aiding them in returning to their home loft (Papi, 1989; Wallraff, 2005; Gagliardo *et al*., 2013). These abilities may reflect an enhancement of mechanisms and capabilities originally present in their wild ancestor. As reviewed by Bonadonna and Gagliardo (2021), many bird species use olfactory cues to orient their spatial courses, and it is possible that others do so as well, including the Rock Dove, from which homing pigeons are descended. The recent development of new tracking technologies, which have already been tested on pigeons in a natural context (Smith *et al.*, 2025), now enables studies that were nearly impossible 20 years ago. These technologies allow for the collection of detailed information about the spatial ecology of Rock Doves and could facilitate the testing of specific hypotheses regarding their orientation mechanisms by using displacement experiments. For instance, it is now feasible to investigate the use of olfactory cues for navigation in unfamiliar areas or to examine the effects of magnetic disturbances on Rock Doves released under completely overcast conditions to verify the existence of a magnetic compass.

The individuals used in the experimental tests reviewed here belonged to colonies where birds showing phenotypic signs of genetic introgression from domestic breeds or feral populations were either absent or reduced to very low percentages (Baldaccini, 2020; Table 1). Unfortunately, genetic introgression from these pigeons into Rock Dove colonies has now become a conservation concern, placing them at risk of genetic extinction. This issue has already been discussed extensively by Johnston et al. (1988), and Johnston (1992) predicted the genotypic extinction of the Rock Dove in the Mediterranean area within the last century. Across Europe, finding colonies of non-introgressed Rock Doves is now nearly impossible (but see Smith *et al*., 2022), thus limiting future experimental opportunities in the range of *Columba l. livia.* Studies could potentially focus on other subspecific populations in regions where non-introgressed colonies still survive. This may be the only residual possibility to shed light on the origins of orientation abilities seen in modern homing pigeons.

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