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ORIGINAL PAPER

Timing and flight mode of departure in migrating European bee-eaters in relation to multi-scale meteorological processes

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Abstract Understanding departure decisions of migratory birds and the environmental factors affecting them is important for predicting their distribution, abundance, and arrival times to breeding and wintering areas. In the past, methodological difficulties to obtain fine-scale bird departure and meteorological data have limited testing the multi-scale effects of meteorology on bird departure during migration. We investigated departure timing of European bee-eaters (*Merops apiaster*) staging in southern Israel, identified their departure flight mode (flapping or soaring) using radio telemetry, and measured local meteorological conditions to study if bird departure was affected by these. Departure timing was examined using a timescale analysis design. The conditions before, during, and after the time of departure were compared using timescales of 24 h, 6 h, 1 h, and 10 min and in relation to bird flight mode. At the between-days timescale, barometric pressure at departure time was significantly lower compared with 2–1 day earlier, whereas temperature at departure was significantly higher compared with 3–2 days earlier. Temperature at departure was also higher compared with 6 h and 3–2 h earlier. Tailwind assistance had no significant effect at any timescale. Soaring birds departed at significantly higher temperature compared with flapping birds. We suggest that bee-eater departure is tuned to the infrequent passage of warm atmospheric depressions at the between-days timescale and with an increasing temperature trend within these days enabling the birds to use energetically cheap soaring flight. We thus suggest that energetic considerations dictate the departure decisions of migrating European bee-eaters.

Keywords Arava Valley · Atmosphere dynamics · Biotelemetry · Bird migration · Cross-country flight · Decision rules

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Introduction

The migratory timing of birds appears critical for their reproductive success and survival (Alerstam and Lindström 1990; Piersma et al. 1990; Fransson 1995; McNamara et al. 1998; Clark and Butler 1999). During their migration journeys, individual birds have to decide on a daily basis whether and when to depart from staging sites based on local meteorological conditions (Gatter 1992; Bauer et al. 2008; Shamoun-Baranes et al. 2006) and their physiological condition (Dierschke and Delingat 2001; Goymann et al. 2010). Their departure time is critically important because it determines the environmental conditions encountered during the following cross-country flight, thereby affecting migration speed and energy expenditure (Alerstam and Hedenström 1998; Bowlin and Wikelski 2008) sometimes over hundreds or even thousands of kilometers (Piersma and Jukema 1990; Clark and Butler 1999; Gill et al. 2009; Shamoun-Baranes et al. 2010a). Moreover, bird fitness may be hampered if, for example, breeding time following migration does not match the seasonal peak in food abundance due to late arrival (Both et al. 2006). In light of the ongoing climate changes affecting long-distance migrants (Jonzen et al. 2006; Devictor et al. 2008), we urgently need to identify the mechanisms underlying the timing of migration in relation to various environmental factors.

Migrating birds may encounter tailwinds or headwinds in a magnitude comparable to their own air speed (Gauthreaux 1991; Liechti and Bruderer 1998; Biebach et al. 2000); hence, a bird coordinating its flight to favorable tailwinds can progress faster and substantially reduce its energetic flight costs (Liechti and Bruderer 1998). Nocturnally migrating passerines and waders that primarily use flapping flight may escape deteriorating headwinds by flying in an atmospheric stratum where favorable winds prevail (Richardson 1978, 1990; Gauthreaux 1991; Bruderer and Liechti 1995). Yet, soaring migrants must remain within the planetary boundary layer because they rely on thermals that are created and later on dissipate within this layer (Stull 1988; Kerlinger and Moore 1989).

Atmospheric processes that are relevant to migrating birds span over several temporal scales (Stull 1988; Kerlinger and Moore 1989; Shamoun-Baranes et al. 2010b). Specifically for springtime (northward moving) migrants in the northern hemisphere, departure from staging sites was found to coincide with processes occurring during several different meteorological timescales. The passage of barometric lows during which wind and ambient temperature may change dramatically occurs at a synoptic scale lasting for several days (Richardson 1978, 1990; Alonso et al. 1990a; Liechti 2006). Sea breeze and other mesoscale processes may also affect migrating birds en route (e.g., Dinevich and Leshem 2002), as well as micrometeorological processes such as the development of convective turbulence when temperature increases (Kerlinger and Moore 1989; Shannon et al. 2002). Yet, in most studies, it is not clear which meteorological factors the birds actually respond to and at which timescales because most studies on departure decisions did not consider explicitly the scale of meteorological processes that may affect departing migrants. Consequently, examination of individual birds' departure timing in relation to different meteorological processes occurring over several temporal scales is critically missing.

Migrating birds usually encounter headwinds when passing over southern Israel during spring (Bruderer and Liechti 1995; see also "Species and study area" in "Materials and methods"). We use this environmental scenario that we term "headwind trap" to explore the multi-scale effects of meteorological conditions on departure timing in the European bee-eater (*Merops apiaster*), a small (~55 g), long-distance migrant that fly by using both flapping and soaring flight modes (Fry 1984). We attached miniaturized radio transmitters to bee-eaters, followed them in the field, and continuously recorded their radio signals, allowing the identification of their flight mode based on radio signal patterns (see "Materials and methods" and Sapir et al. (2010)). We used four different timescales (24 h, 6 h, 1 h, and 10 min), both before and after departure, over which we tested for the effects of wind, temperature, and barometric pressure on bird departure, using high-rate local meteorological measurements. We tested for synoptic, mesoscale, and microscale effects following their conventional meteorological timescales (Fujita 1986; Stull 1988). Effects related to synoptic-scale meteorological dynamics, for example, the passage of barometric lows, were examined using a timescale of 24 h. Mesoscale-related effects, such as sea breeze (e.g., Dinevich and Leshem 2002) and the gradual development of convective thermals during the morning (e.g., Alonso et al. 1990b), were tested using 6 and 1 h timescales. Micrometeorological processes were tested using the most detailed meteorological data available to us (10-min data). We furthermore examined if meteorological conditions differed between flapping and soaring birds at the time of departure.

We hypothesized that migrating birds would coordinate their departure for cross-country flight in relation to tailwind assistance and predicted that departure will take place in times during which tailwind blows or when headwind subsides (i.e., when no headwind trap prevails). We also hypothesized that soaring flight will be used under conditions of high ambient temperatures that are known to induce thermal updrafts (Kerlinger and Moore 1989; Alonso et al. 1990b). We note that, in this work, we focus only on departure decisions of European bee-eaters and we therefore deal only with relevant, limited spatial and temporal domains. We studied the birds' post-departure flight behavior en route in a separate, complementary work (Sapir 2009).

Materials and methods

Species and study area

The European bee-eater is an agile insectivorous bird that breeds throughout the southern parts of Europe and Western to Central Asia and winters south of the Sahara (Fry 1984; Snow and Perrins 1998). Bee-eaters are known to migrate both nocturnally and diurnally and to use both flapping and soaring flight modes (Fry 1984; Shirihai 1996). The species is a common summer breeder in central and northern Israel and a very common passage migrant during both autumn and spring throughout the entire country (Shirihai 1996). Large bee-eater flocks pass through southern Israel, where the species do not breed, as part of the Eurasian–East African migration system, one of the five major global flyways for soaring birds (Newton 2007), with daily records of up to 4,700 springtime migrants concentrated in the southern part of the Arava Valley (Shirihai 1996; Yosef 2004).

The Arava Valley—the southern part of the Great Rift Valley in Israel, between Eilat and the Dead Sea (Fig. 1)—is an extremely arid region with an average annual precipitation of 30–50 mm (Eshbal 1950). The synoptic conditions prevailing in the southern part of the Arava Valley during spring are characterized by moderate northern winds in the boundary layer (Bitan-Buttenwieser 1971; Ziv 1994). Specifically, in the southern part of the Arava Valley, northern surface winds predominate during 80% of the time, compared with 50–60% in the valley's mid-section (Bitan-Buttenwieser 1971), making this area a headwind trap. The occasional (once in 11 days on average during 2005 and 2006), short term (~ 2 days) passage of barometric lows through the area alters the local meteorological conditions, particularly when the depression's warm section influences the area. During these times, the temperature increases and the northern wind alleviates and sometimes even reverses. As the depression moves eastwards, a transition to humid westerlies occurs, and later on the northern wind returns to prevail (Ziv 1994). Springtime bird migration within the boundary layer in the southern Arava Valley thus necessitates flight against headwinds throughout the season (Bruderer and Liechti 1995), with the exception of infrequent passage of warm large-scale weather systems through the area.

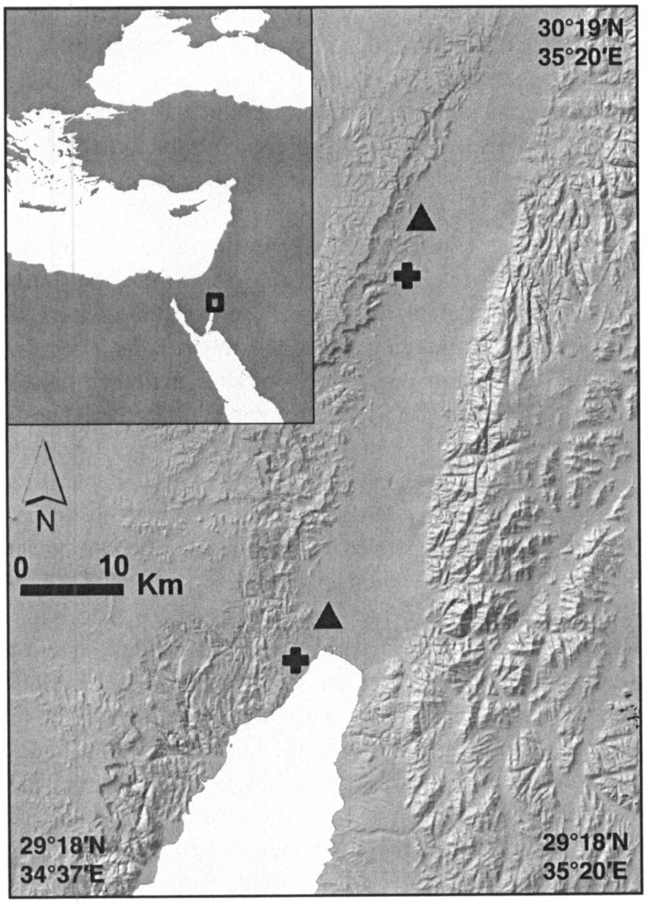


Fig. 1 The location of the two study sites (*black triangles*) and the meteorological stations (*plus signs*) in the southern Arava Valley in the south of Israel, just north of the Gulf of Aqaba of the Red Sea. Eilat is the more southern site

The study was done in two sites (Fig. 1) during the course of the bee-eaters' spring migration in 2005 and 2006. From the end of March to mid May, birds were studied in the surroundings of Eilat (29°34′ N, 34°58′ E), while from mid to end of May, when bee-eaters' abundance decreased in Eilat, we shifted our study 40 km northwards to the surroundings of Grofit (29°56′ N, 35°04′ E). The large concentrations (at least several hundreds of individuals at a given time) of staging European bee-eaters in these two localities are likely due to high local food availability around melon (*Cucumis melo*) and watermelon (*Citrullus lanatus*) agriculture where European honey bees (*Apis mellifera*) serve as pollination agents (Yosef 2004; Yosef et al. 2006).

General methodology

European bee-eaters were trapped with mist nets in agricultural fields near bee hives or in large Rybachy traps (Erik 1967) in the Switzerland Park of the International Birding and Research Centre in Eilat. Mist nets (12 × 2.5 m) were set only in the early morning and late afternoon hours to minimize the exposure of the birds to intense radiation and high ambient temperatures, and the nets were regularly visited every 10 min to minimize the time over which bees might sting a bird trapped in the net. Rybachy traps, located far away from bee hives, were regularly visited every 0.5 h. Trapped birds were ringed and were individually marked by human hair lightener (Blondor Light Powder, Wella Corporation, Woodland Hills, CA, USA) that was applied for 10 min to the tips of two to three of their flight feathers to enable their identification in the field (White et al. 1980). After applying the lightener, we washed all the remains of the lightener from the feathers with water and let the feathers dry. Then, the birds were equipped with a 1-g radio transmitter operating at the 605 MHz band (0.2×0.7×0.3 cm; SP2000-HR, Sparrow Systems, Fisher, IL, USA). The transmitter mass was 2.05% of the body mass of the bird with the lowest body mass (48.8 g) tagged and 1.78% of the average body mass of all the birds (56.3 g). The transmitters emitted continuous signal amplitude that was frequency modulated by heart muscle potentials (see Cochran and Wikelski (2005) for technical details). The transmitters had a 9-cm flexible wire antenna that was 0.8 mm in diameter. The birds were anesthetized in the field with a mixture of isoflurane (Abbott Laboratories, North Chicago, IL, USA) and air in order to keep their distress at a minimum and not cause pain (Cochran and Wikelski 2005). Following Raim (1978), a patch of approximately 2 cm^2 of back body plumage close to the birds' center of gravity was cut to the feather stumps and the heart rate transmitter was glued to a <2-cm^2 cloth. The cloth was then glued onto the feather stumps on the back of the bird with eyelash adhesive (Andrea Eyelash Adhesive, Los Angeles, CA, USA). Two wire electrodes were placed under the skin using a blunt needle (see Cochran and Wikelski (2005) for a detailed description of the attachment procedure).

Birds were released back to the wild near (< 50 m) conspecifics, and we minimized bird handling time by releasing the birds as soon as possible after completing the ringing and transmitter attachment procedures, within 1 h from the time of trapping. We followed the birds after their release using the radio tracking system and visually using binoculars. We could not detect an apparent change in the behavior of radio-tagged birds, identified by their light feather tips: they foraged, flew, and continued to interact socially after their release. The same was found also during migratory flights when several of the birds were occasionally spotted using binoculars within bee-eaters flocks consisting of several dozens of individuals, during which the tagged individuals were found inside the flocks and did not lingered behind and no difference in their flight could be visually detected using binoculars. Three of the tracked birds were trapped twice, 3 (two birds) and 4 days after being equipped with radio transmitters, and in all cases no signs of infection were seen upon visual inspection of their backs. The same tags were applied to ~17-g spotted antbirds (*Hylophylax naevioides*) that are more than three times lighter than bee-eaters and no adverse effects of the tag could be detected (Steiger et al. 2009). Raim (1978) measured the time it took similar tags to fall off from the back of 60 brown-headed cowbirds (*Molothrus ater*) and estimated that the average time is 10–14 days, with an upper limit of 24 days.

We followed the birds using two vehicle-mounted radio telemetry systems that included a radio receiver (AR3000; AOR Ltd., Tokyo, Japan), a GPS device (Garmin 12XL, Garmin, Olathe, KS, USA), and a digital compass (Revolution 2x, True North technologies, Maynard, MA, USA) positioned on custom-made directional yagi antennas. Yagi antennas included an array of four 12-element antennas in one vehicle and a single hand-held 12-element antenna in the second vehicle in 2005 and a single 17-element antenna in one vehicle and two 12-element antennas in the second vehicle in 2006 (Cochran and Pater 2001). To determine bird flight mode during departure, we used the wing flap and null reception signals as soaring flights were characterized by absence of wing flaps and a unique signature of sinusoidal signal strength because of null reception when the position of the transmitter was 180° and 360° relative to the receiving antenna (see Sapir et al. (2010)). The null reception pattern that characterizes soaring flight was verified by direct observations and is also known from tracking of soaring birds elsewhere (e.g., Cochran 1975).

Eleven tagged birds were tracked throughout their stopover periods spanning from half a day (i.e., a bird that was tagged in the afternoon and departed the following morning) to 9 days. Three other birds staged in the area for at least 11 days before their tags' batteries were exhausted. We could not locate another bird during the first night following its trapping and this bird might have departed for migration during the night, its transmitter may have stopped functioning, or it may have been taken by a predator beyond the range of our tracking system. For the 11 individuals included in the following analysis, we recorded the exact time of departure for migratory cross-country flights in 1-min accuracy. We distinguished departure for cross-country flight from local movements by following the birds along their migration routes, well beyond the borders of their agricultural staging sites, and tracked the birds for 25 to 230 km from their stopover sites until their signals were lost (see Sapir (2009) for information on the birds' post-departure behavior en route).

To assess the local meteorological conditions, we used meteorological measurements from two meteorological stations that were operated by the Israeli Meteorological Service (IMS). The station in Eilat was positioned 2.5 to 8.5 km south of the departure localities of the Eilat birds, and the station in Grofit was located about 6 km south of the departure localities of the Grofit birds (Fig. 2). Both stations are situated within the Arava Valley, with <20-m elevation differences between the stations and the birds' departure localities. The meteorological measurements included wind direction and speed measured at 10 m above the ground by a rotational anemometer (05103-LC Wind Monitor for MetData1, R. M. Young, Traverse City, MI, USA), as well as temperature (C°) measured at 2 m by a temperature probe (MP101A, Rotronic, Bassersdorf, Switzerland). Meteorological data were logged by the IMS in 10-min intervals throughout the study period. At the time of departure for cross-country flight, we were able to directly observe six of the tracked birds using binoculars. The birds departed from trees and electricity wires at altitudes <10 m above ground, justifying our use of near-surface meteorological observations.

We transformed wind data (direction and intensity) into a single biologically meaningful, variable termed tailwind assistance (TWA; see Piersma and Jukema 1990; Fransson 1998; Åkesson and Hedenström 2000; Dänhardt and Lindström 2001; Dierschke and Delingat 2001; Delingat et al. 2008). TWA was calculated by the following formula:

$$\mathrm{TWA} = V_w \cdot \cos\left(\left(\theta_w + 180^\circ\right) - \theta_b\right), \quad (1)$$

where V_w is the measured wind velocity in meter per second, θ_w is wind direction (i.e., the direction from where the wind was blowing) in degrees, and θ_b is the presumed direction of the birds. TWA is simply the tailwind component of wind velocity in meter per second or the wind assistance vector at the presumably preferred direction of the bird, with positive and negative values indicating tailwinds and headwinds, respectively. Since the tracking ended before the birds reached their destination, we have no information about the true heading to the destination of each tracked bird. We consequently used the average of the points where we lost the tracked birds during flight, which was concentrated in the north compass direction (Fig. 2; average vector μ=359°, length of mean vector r=0.94; Rayleigh's test: N=11, Z=9.72, P<0.001), as the presumed heading of European bee-eaters migrating in this area during spring. Using θ_b of 0° for convenience, Eq. 1 simplifies to:

$$\mathrm{TWA} = V_w \cdot \cos\left(\theta_w + 180^\circ\right). \quad (2)$$

In addition to wind and temperature data available from local weather stations, we also used barometric pressure in 1-h intervals, measured at 2 m above the ground by a barometer (Nova, Princo Instruments Inc., Southampton, PA, USA) by the meteorology unit of the Jacob Blaustein Institutes for Desert Research (Ben-Gurion University) in Sede Boqer, 140 and 100 km north of Eilat and Grofit, respectively. These pressure data from Sede Boqer are highly correlated with pressure data from Eilat (major axis model II regression, n=1404, r=0.89, p<0.0001, coefficient ± SD=1.25±0.017, intercept = −186.8±16.57). We used the data from Sede Boqer because the pressure data from Eilat were available only at 3-h intervals, precluding the examination of barometric pressure effects at 1-h resolution. Compared with the other meteorological variables used, barometric pressure tends to vary much less at these spatial scales (e.g., Miller et al. 1999).

Statistical analyses

To assess the effects of meteorological conditions on bird departure, we compared the meteorological conditions in the staging site at the time of bird departure with specific times before and after departure. This was done following Dänhardt and Lindström (2001), who compared the con-

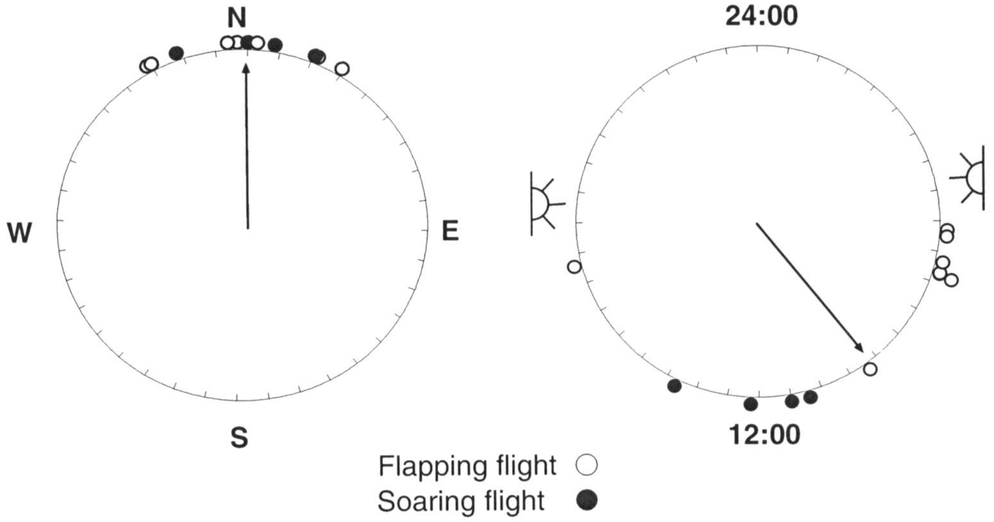


Fig. 2 Direction and timing of departure for cross-country migratory flight observed in 11 European bee-eaters tracked in the southern Arava Valley, Israel, during the springs of 2005 and 2006. *Left*, the distribution of track directions defined as the vector originating at the departure location and pointing at the location where the signals of the bird were lost. *Right*, the distribution of departure times from the stopover sites throughout the daily cycle, starting at 24:00 local time (UTC + 2) clockwise. *Symbols* to the right and left of the right diagram indicate the average sunrise and sunset times during the study period, and *arrows* indicate the mean of the distributions

ditions between different days so that the conditions at the day of departure were compared with the conditions during 2 and 1 day before and 1 day after departure. Our tracking procedures enabled us to pinpoint the time of departure in 1-min resolution while the meteorological data were available at 10-min resolution for wind and temperature and at 1-h resolution for barometric pressure. We consequently were able to apply the approach of Dänhardt and Lindström (2001) at a much finer temporal resolution and to address issues of both scale (e.g., bird response to variation between days, hours, or minutes) and resolution within scale (bird response to conditions spanning over one, two, or three time intervals before departure). For this purpose, we applied a timescale analysis design using meteorological data spanning over four different timescales of 24 h, 6 h, 1 h, and 10 min. For example, to apply the 10-min timescale to the bird carrying ring number CC29987 that departed at 09:37 on 12 April 2005 from Eilat, we compared the meteorological conditions measured during the exact time of departure at the 10-min timescale (i.e., 09:30–09:40) to the conditions during each of the three 10-min intervals preceding departure (i.e., 09:00–09:10, 09:10–09:20, 09:20–09:30) and the 10-min interval following departure (i.e., 09:40–09:50). We denote the sequence of the five times relative to departure time as −3, −2, −1, 0, and +1 and repeated the same approach for the rest of the birds using this timescale and also using the 1 h, 6 h, and 24 h timescales. Overall, we examined the association of meteorological conditions and bird departure over more than two orders of magnitude before (10 min to 72 h) and after (10 min to 24 h) departure.

We used repeated measures analysis of variance (RM-ANOVA) to compare conditions within each of the four different baseline timescales and carried out separate tests for each meteorological factor (TWA, temperature, and barometric pressure, excluding the 10 min timescale analysis for the latter variable). In these analyses, we treated time as a within-subject factor (time) and bird flight mode (flight mode; either soaring or flapping) as a between-subject factor. Following Zar (1996) and Garson (2009), we applied Dunnett's tests for comparing the conditions at the time of departure to those measured at other times using four pairwise comparisons between times −3, −2, −1, and +1 and the control time (0, the time of departure). Dunnett's test is a planned comparison variant specifically designed to compare a control group to treatment groups while not comparing statistics between different treatments. Unlike ordinary planned comparisons, the number of groups (k) is considered in determining the critical value of Dunnett's test statistic (q'); thus, the significance level of this test is adjusted to the number of comparisons (Zar 1996). Given our interest in specific comparisons (departure time *versus* other times), the combination of RM-ANOVA and the followed up Dunnett's test results was used in making statistical inferences. Rayleigh's tests were carried out following Batschelet (1981). We additionally used independent-samples t-tests to compare the meteorological variables measured at the time of departure between flapping and soaring birds.

To examine the effects of all the meteorological factors in determining the probability of departure for cross-country flight in a single statistical model, we applied multi-factorial conditional logit analyses using SPSS Cox regression (Garson 2009). The dependent variable in this test was dichotomous: the bird either staged (before departure) in which case the variable's value was 0 or departed for migration in which case the variable's value was 1. Unlike in previous analyses, in this analysis we used measurements from two and one time intervals preceding departure (coded 0) and measurements from the time of departure (coded 1). Similar to previous analyses, a separate model was fitted for each timescale. Increasing the number of time intervals before and after the time of departure included in this analysis would have substantially increased the unbalanced ratio between the two types of the dichotomous response variable, which may increase the probability of making a type II error that is the failure to observe a true effect (a difference) due to poor sensitivity (Cramer 1999). All of the statistical analyses were computed using SPSS 15.0 (SPSS 2006) and were two-tailed tested.

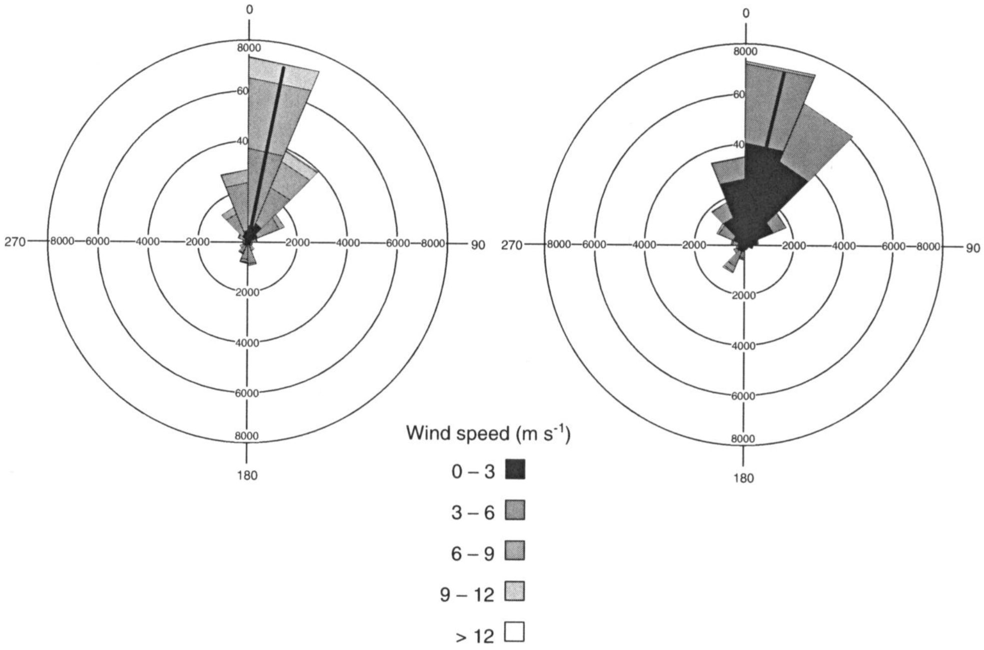
Results

General results

Mean wind vector (μ) and length of mean vector (r) in Eilat ($\mu=12.4°$, $r=0.64$) and Grofit ($\mu=10.7°$, $r=0.68$) during the springs of 2005 and 2006 were concentrated in a northern direction (Fig. 3, Rayleigh test: $Z=14{,}140.8$, $N=26{,}199$ 10-min observations, $P<0.001$, and $Z=10{,}857.5$, $N=30{,}804$ 10-min observations, $P<0.001$, respectively, for Eilat and Grofit; Batschelet 1981). Eilat was characterized by higher prevalence of strong northerly winds compared with Grofit (Fig. 3) and, consequently, average tailwind assistance in Eilat throughout the study period (mean ± SD -3.7 ± 3.8 m s^{-1}) was significantly lower (independent samples t-test: $t=53.4$, $df=56{,}995$, $P<0.001$) than in Grofit (-2.3 ± 2.5 ms^{-1}). It is not clear, however, if the rather small absolute average difference in tailwind assistance (1.4 ms^{-1}) has any biological importance to birds that migrate through the area. Overall, these data confirm the headwind trap scenario experienced by spring migrants in the study area (Bitan-Buttenwieser 1971; Ziv 1994; Bruderer and Liechti 1995).

Spring migrating European bee-eaters tracked in southern Israel at 2005 and 2006 departed for cross-country flights

Fig. 3 The distribution of wind direction (i.e., the direction from which the wind is blowing) and speed throughout the springs of 2005 and 2006 in Eilat (*left*) and Grofit (*right*) based on 10-min measurements throughout the entire study period. The mean wind directions are indicated by a *thick black line* in each subplot and each *circle* is indicated by its frequency



during daytime hours, and their departure times were not random (Fig. 2; average vector μ=09:31, length of mean vector r=0.67; Rayleigh's test: N=11, Z=4.94, P=0.006). The birds departed under diverse meteorological conditions: seven birds departed for cross-country flight under opposing northern winds of up to 7.2 ms^{-1}, whereas the remaining four birds were assisted by tailwinds (Fig. 4a). Most birds assisted by tailwinds departed using soaring flight, while most birds that departed against headwinds used flapping flight (Fig. 4a). Most soaring departures took place at relatively high ambient temperatures compared with flapping departures (Fig. 4b). TWA and barometric pressure were significantly negatively correlated (r=−0.28, P<0.001), while TWA and temperature were significantly positively correlated (r=0.44, P<0.001) at the 10-min timescale.

Tailwind assistance and bird departure

At the 24 h timescale, no significant variation in TWA in relation to time was detected and consequently no pairwise Dunnett's comparisons (between departure time and other times relative to departure) were made (Table 1). In this timescale, TWA varied significantly in relation to flight mode (the between-subject factor flight mode in Table 1). At the 6 h, 1 h, and 10 min timescales, RM-ANOVA revealed significant variation in TWA in relation to the time of the measurements (Table 1), yet no single pairwise Dunnett's comparison was significant (P>0.05). No significant variation in TWA was found in relation to bird flight mode at all three timescales. Mean (± SE) TWA recorded at the time of departure of flapping birds was −2.5 (± 1.0) m s^{-1} and not significantly different (independent samples *t*-test: t=1.87, N_1=7, N_2=4, P=0.094) from that recorded during the departure of soaring birds (1.5±1.0 ms^{-1}).

Barometric pressure and bird departure

At the 24 h, 6 h, and 1 h timescales, RM-ANOVA showed that barometric pressure varied significantly with time (Fig. 5, Table 1), and pairwise Dunnett's comparisons show a significantly higher barometric pressure 48 and 24 h before departure compared with barometric pressure at departure (q'=3.78 and q'=4.00 for 48 and 24 h, respectively, k=5, df=40, P<0.01 for both). At the 6 and 1 h timescales, not a single pairwise Dunnett's comparison was significant (P>0.05). In the analyses of all three timescales, the effect of bird flight mode was not significant. Mean (± SE) barometric pressure at the time of departure of flapping birds (956.2±0.7 mbar) was not significantly different (t=0.7, N_1=7, N_2=4, P=0.5) from that recorded during the departure of soaring birds (957.0±0.3 mbar).

Temperature and bird departure

At the 24 h, 6 h, 1 h, and 10 min timescales, RM-ANOVA revealed that temperature varied significantly with time (Fig. 6; Table 1). At the 24 h timescale, pairwise Dunnett's comparisons show that temperature at 72 and 48 h before departure was significantly lower compared with temperature at departure (q'=3.22 and q'=2.82 for 48 h and 72 h, respectively, k=5, df=36, P<0.05 for both) and in this timescale bird flight mode was also significant (Table 1). At the 6 h timescale, pairwise Dunnett's comparisons showed that temperature at 6 h before departure was significantly

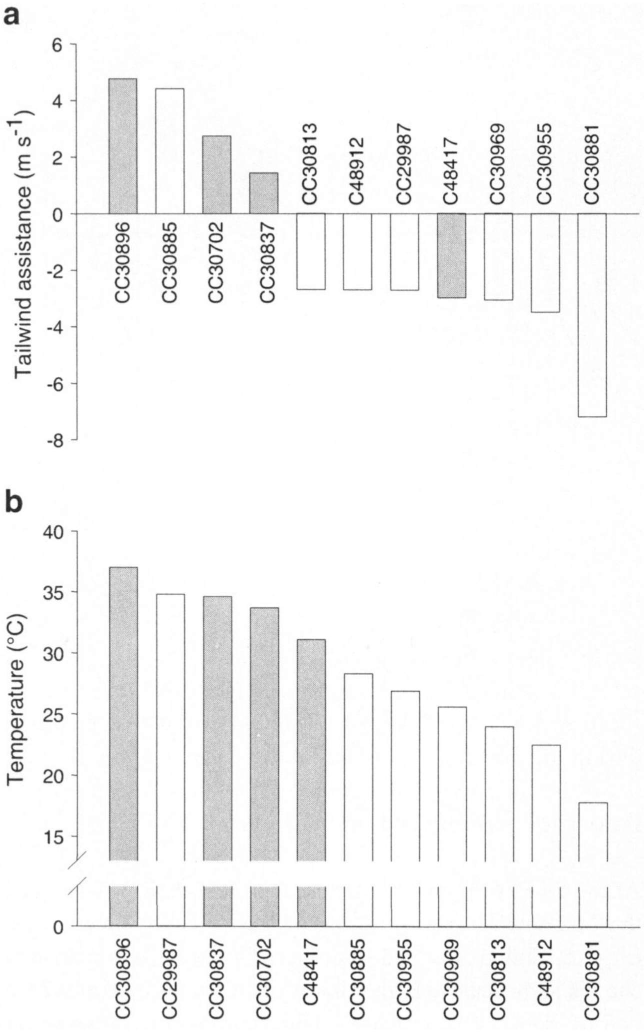


Fig. 4 **a** The distribution of tailwind assistance, the tailwind component of wind velocity for a given wind direction at departure, and **b** the distribution of temperatures at departure, calculated for 11 European bee-eaters taking off for cross-country flight in southern Israel during the springs of 2005 and 2006, presented in descending order. *Gray bars* depict birds that engaged in soaring during departure and *white bars* indicate flapping birds

lower compared with temperature at departure ($q'=2.97$, $k=5$, $df=36$, $P<0.05$), while flight mode was not a significant factor in this timescale. At the 1 h timescale, pairwise Dunnett's comparisons showed a significantly lower temperature at 3 and 2 h before departure compared with the temperature at departure ($q'=4.64$, $k=5$, $df=36$, $P<0.01$ for 3 h and $q'=3.02$, $k=5$, $df=36$, $P<0.05$ for 2 h), while at the 10 min timescale not a single pairwise Dunnett's comparison was significant ($P>0.05$). Flight mode was a significant factor in both 1 h and 10 min timescales. Mean (± SE) temperature at the time of departure of flapping birds (26.3±1.5°C) was significantly lower ($t=2.9$, $N_1=7$, $N_2=4$, $P=0.017$) compared with the temperature at the time of departure of soaring birds (34.4±0.7°C).

Multi-factorial tests of meteorological effects on bird departure

The conditional logit analysis showed that, at the 24 h timescale, barometric pressure was the only significant explanatory factor, with higher pressure during 48 to 24 h before departure compared with departure time (Wald $\chi^2=4.26$, $df=1$, Exp(B)=1.38, $P=0.039$), whereas both temperature and TWA had no significant effect ($P>0.15$). At the 6 h and 10 min timescales, no meteorological factor had a significant effect on bird departure ($P>0.15$ for all meteorological variables). At the 1 h timescale, temperature was a significant explanatory factor, with lower temperature 2 to 1 h before departure compared with the time of departure (Wald $\chi^2=3.84$, $df=1$, Exp(B)=0.68, $P=0.05$), whereas TWA and barometric pressure had no significant effect ($P>0.28$).

Discussion

Spring-migrating European bee-eaters departed from staging sites in southern Israel for long distance cross-country flight at variable meteorological conditions; yet bee-eaters were found to time their departure in relation to specific

Table 1 The effects of meteorological factors on bird departure timing and flight mode tested by repeated-measures ANOVA and Dunnetts' tests

Meteorological factor	Tailwind assistance				Temperature				Barometric pressure		
Timescale	24 h	6 h	1 h	10 min	24 h	6 h	1 h	10 min	24 h	6 h	1 h
RM-ANOVA results (P)											
Time	NS	0.014	0.006	<0.001	<0.001	<0.001	<0.001	0.005	0.002	0.001	0.018
Flight mode	0.026	NS	NS	NS	0.021	NS	0.020	0.016	NS	NS	NS
Time × flight mode	NS	NS	<0.001	<0.001	0.022	0.003	NS	NS	NS	NS	<0.001
Significant ($P<0.05$) Dunnetts' pairwise comparisons (number of groups, $k=5$)	–	–	–	–	−72 h, −48 h	−6 h	−3 h, −2 h	–	−48 h, −24 h	–	–

NS not significant ($P>0.05$)

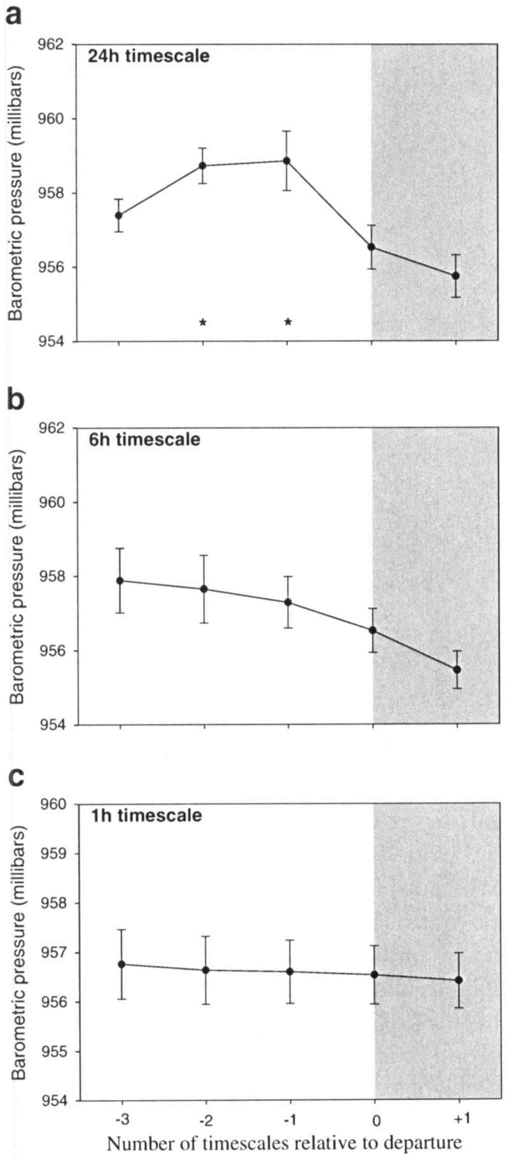


Fig. 5 The average±SE barometric pressure at 24- (**a**), 6- (**b**), and 1-h (**c**) timescales before (−) and after (+) departure time (*0*). Post-departure time is shaded *gray*. *Asterisks* denote significant statistical differences in barometric pressure between a certain time and departure time ($P<0.05$)

meteorological variables at certain timescales. Moreover, bee-eaters that departed using flapping flight differed significantly from soaring birds in their departure conditions. Contrary to our expectation, tailwind had no discernable effect on bee-eater departure timing in all timescales, whereas barometric pressure and temperature had significant effects at different timescales. Bird departure time was associated with relatively low barometric pressure compared with the preceding 1–2 days. Temperature was relatively high at departure compared with the preceding 2–3 days as well the preceding 6 and 2–3 h. Departure by soaring flight was carried out under substantially higher ambient temperatures compared with departures made using flapping flight, and similar differences in temperature between these two flight modes were found at both coarse (24 h) and fine (1 h and 10 min) timescales. We therefore suggest that European bee-eaters may integrate information on changes in meteorological conditions across several timescales to synchronize, in a fairly fine resolution, their departure from spring stopover sites in southern Israel that are characterized by headwind trap.

The observed departure times of the bee-eaters correspond well with synoptic circumstances associated with the short-term (ca. 2 days) passage of barometric lows through the area that induce high temperatures and increase the southern component of the wind, altering the otherwise rather stable conditions of higher pressure, lower temperature, and northern winds. These short-term opportunities may be used by other migratory species and may be particularly important to birds that are obliged to migrate within the boundary layer. These synoptic circumstances may explain bird response to environmental conditions on a broad scale since similar conditions have been reported, for instance, in southern Sweden during autumn migration (Alerstam 1978; Dänhardt and Lindström 2001) and in northern Scotland during spring migration (Delingat et al. 2008), affecting both migratory volume and departure decisions of migrating birds en route.

Our results suggest that a trend of increasing temperature and decreasing barometric pressure lasting a few days can potentially provide a reliable cue for the birds to adjust their digestive, muscular, and circulatory systems in preparation for the enduring cross-country flight (Piersma and Lindström 1997; Bauchinger and Biebach 2005). While at the coarse timescale (24 h) the birds may rely on barometric pressure and temperature, at the shorter timescale (6 and 1 h) they may fine-tune their response based only on changes in temperature. High temperature generates convective updrafts that facilitate soaring, a flight mode that is much cheaper energetically compared with flapping in European bee-eaters (Sapir et al. 2010). Undertaking soaring flight throughout many parts of the long-distance (6,000-9,000 km) migration flyway of European bee-eaters (Fry 1984; Snow and Perrins 1998) may substantially lower the energetic cost of the journey, creating a strong selection pressure to depart from staging sites when atmospheric conditions facilitate this mode of flight. Such selection pressure may drive the evolution of sensory abilities to detect trends in ambient temperature and barometric pressure across several timescales, particularly in relation to relatively fine-scale temperature trends at which differences between soaring and flapping birds were most striking (Fig. 6b, c). Kreithen and Keeton (1974) provide evidence that homing pigeons are capable of detecting fine pressure differences in the laboratory, and this may suggest that other avian species, such as the European bee-eater, can sense barometric pressure, although this was never directly tested.

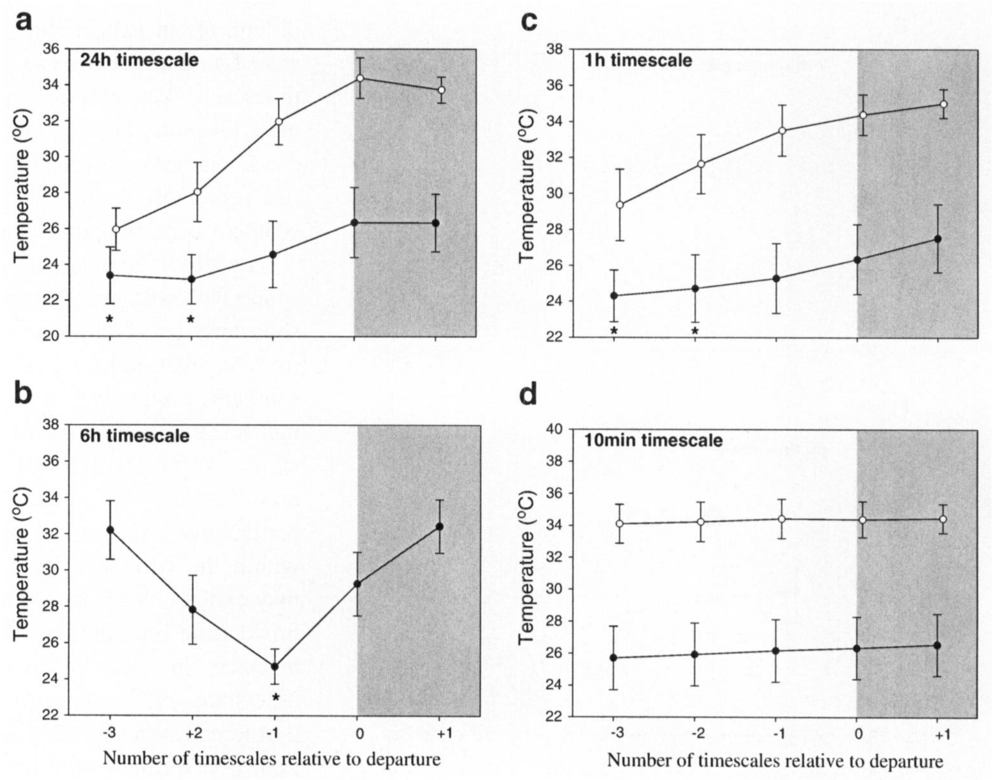


Fig. 6 The average±SE temperature at 24-h (**a**), 6-h (**b**), 1-h (**c**), and 10-min (**d**) timescales before (-) and after (+) departure time (*0*) and in relation to bird flight mode (subplots *A*, *C*, and *D*) with flapping birds' data marked as *filled circles* and data of soaring birds marked as *open circles*. Post-departure time is shaded *gray*. *Asterisks* denote significant statistical differences in temperature between a certain time and departure time ($P<0.05$)

The association between high ambient temperature and the onset of migratory flight is common for both large soaring birds (Andrle 1968; Alonso et al. 1990b) and much smaller butterfly species that regularly soar during long-distance migration (Gibo and Pallett 1979; Gibo 1981). This association may affect the temporal distribution of migratory animals as shown in four soaring migratory butterflies in Florida that their abundance was correlated with temperature and not with wind throughout autumn (Walker and Riordan 1981). Butterflies thus departed for migration when temperatures were high, facilitating the development of convective thermals that were used for soaring.

Contrary to our expectation, TWA was not a significant factor in all of the comparisons made across all timescales. This finding goes in line with several studies that reported no effect of wind on departure timing in small passerine migrants (Fransson 1998; Bulyuk and Tsvey 2006; Bolshakov et al. 2007). Other studies, though, found that tailwind assistance facilitates departure (Åkesson and Hedenström 2000; Dänhardt and Lindström 2001; Dierschke and Delingat 2001; Delingat et al. 2008). Birds may depart regardless of wind assistance if they aim to minimize their migration time such that waiting further for a change in weather may delay their migration and hamper breeding opportunities at the end of the voyage (McNamara et al. 1998; Weber et al. 1998; Liechti 2006). We note that due to the difference in the wind regime between the southern and the middle sections of the Arava Valley in spring (Bitan-Buttenwieser 1971), after escaping from the southern Arava Valley's headwind trap, the birds probably were able to progress northward with some wind assistance or at least with subsided headwinds. Thus, the southern Arava Valley's headwind trap is fairy restricted in extent, unlike other areas where birds may encounter headwinds extending over hundreds and even thousands of kilometers at certain times of the year (e.g., north-western Europe during autumn; Erni et al. 2005).

When migrants that are capable of using either flapping or soaring flight experience ambient conditions that do not allow their use of soaring flight, they may decide to depart using flapping, resulting in temporal separation between flight modes during departure (Fig. 2). Furthermore, if updrafts develop during their flight, they may switch to soaring flight en route. For example, sparrowhawk (*Accipiter nisus*) migration during autumn in southern Sweden was characterized by early morning flapping flights and mid-day soaring flights when updrafts became available (Alerstam 1978). Of the seven bee-eaters that departed for cross-country flight by flapping, six switched to soaring after several dozens of kilometers en route following an increase of temperatures and the development of updrafts (Sapir 2009).

In spring, a temperature threshold was found to limit the departure of migrating *Catharus* thrushes that use flapping flight (Cochran and Wikelski 2005). It has been suggested that in-flight heat costs may be too large under low ambient temperatures or that such conditions may indicate that food abundance, known to be controlled by temperature, is low further to the north, hampering feeding and fuel storage and making further progress due north unprofitable. The latter explanation was also suggested by Bauer et al. (2008) who studied the spring migration of pink-footed geese (*Anser brachyrhynchus*). For diurnally migrating dragonflies in autumn, Wikelski et al. (2006) found that departure was associated with a decreasing temperature trend rather than a temperature threshold and such a trend may be correlated with a synoptic condition of winds that blow to the south (presumable dragonfly destination). Our temperature data indicate that a temperature threshold may exist at the between-day timescale (Fig. 6a), yet at the finer 1 h timescale it appears that a temperature trend rather than a threshold is more likely (Fig. 6c). Thus, bee-eater response (departure) to temperature variation during migration is timescale dependent and suggests a set of rules used by the birds to schedule their travel. We suggest that departures by soaring of bee-eaters took place by combination of temperature peak at the 24 h timescale and steep increase in temperature for several hours. Thus, the bee-eaters' decision rules regarding departure may employ data integrated across several timescales.

The departure decision rules of bee-eaters can be further compared in the future with those of other taxa (e.g., geese and butterflies) during different migration seasons (i.e., spring *vs*. fall) in different latitudes and among years to study how the specific biological context may affect this important aspect of bird behavior. Because the reproductive success of the birds may depend on their time of arrival to breeding areas (Both et al. 2006; Møller et al. 2008; Reed et al. 2009; Watanuki et al. 2009; D'Alba et al. 2010), it is important to quantify bird decision rules (e.g., Bauer et al. 2008), identify the processes responsible for their evolution, and explore their consequences, especially under the current scenario of global climate changes. For example, several simulation studies proposed that future tracks of barometric lows in the northern hemisphere will shift polarwise (McCabe et al. 2001; Yin 2005). More specifically, it has been suggested that storm frequency and intensity over the Mediterranean basin will be reduced over the next several decades (Bengtsson et al. 2006; Pinto et al. 2007). Because bee-eater departure is conditional upon the infrequent passage of depressions through the study area and because the distribution range of the species circumvents the Mediterranean Sea (Fry 1984; Snow and Perrins 1998), future climate changes may potentially disrupt bee-eater migration and consequently harm its populations in a major part of its global distribution range.

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Ethical standards Bird trapping permits were obtained from the Israeli Nature and Parks Authority (permits 2005/22055, 2006/25555) and the experimental procedure was approved by the Animal Care and Use Committee of the Hebrew University of Jerusalem (permit NS-06-07-2).

Conflicts of interest The authors declare that they have no conflicts of interest.

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