Body condition as a determinant for stopover in bee-eaters (*Merops apiaster*) on spring migration in the Arava Valley, southern Israel

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Abstract

The most critical, and dangerous, time of the avian life cycle probably is the migratory period when not only does a migrating bird have to decide on the routes to take to and from the wintering grounds but also when to rest, where and for how long. To understood the migrants decision we studied migratory European Bee-eaters (*Merops apiaster*) along the Arava Valley, Israel, during their spring migration stopover immediately after crossing the combined ecological barrier of the Sahel, Sahara, and Sinai deserts. We evaluated the effects of body mass and age on the decision to stopover as a function of the distance from the northern edge of the deserts northwards up to the Dead Sea basin. We propose a new "drop-out hypothesis" wherein the weaker individuals dropout earlier from a migratory flock that is moving northwards from an ecological barrier. Most of the birds that drop out at the stopover sites closest to the ecological barrier are juveniles, on their first migration from Africa and that lack experience of the northbound flight. The proportion of adults increases as the flock moves northwards. The evolutionary and conservation implications of this study stress the importance of conservation of not only a single stopover site along the migratory route but

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that of several points staggered out such that they will allow individuals with varying degrees of body condition to advance in their desired direction with minimum stress.

1. Introduction

Birds fly long distances to accomplish their annual migrations in the spring and autumn. For many species it is achieved by making a series of long distance flights interrupted by staging stops when their body stores are replenished (Alerstam and Lindstrom, 1990; Nolet and Drent, 1998). Pennycuick (1989) showed that flight energy cost increased with increasing body mass resulting in the birds having to decide where to stop and for how long. A wide range of theoretical (e.g. Weber et al., 1998) and field studies (e.g. Fransson, 1998) have supplied varying answers to the dilemma of how birds make their stop-over decisions; when, where and for how long. This can become especially critical before or after the crossing of extensive ecological barriers such as a desert or a large water body wherein they cannot forage and thus depends exclusively on their energy stores and metabolic water (Biebach et al., 1986; Carmi et al., 1992; Biebach, 1995).

Models of stopover ecology of migrants have up to now emphasized stopover duration, body mass gain rate, and optimal wind conditions for their continued migration (e.g. Biebach, 1995; Weber et al., 1998; Liechti and Bruderer, 1998). However, it remains unanswered as to which parameter dictates where an individual decides to stopover.

Based on over a decade of research at Eilat, Israel, (e.g. Yosef and Tryjanowski, 2002a, b; Yosef et al., 2002, 2003), we reasoned that from a migratory flock that had just accomplished the crossing of the deserts, the individuals in the flock would try and reach appropriate stopover areas as close to their breeding grounds in the north as possible. This would be a function of the energy efficiency of the individual during the passage over the inhospitable deserts, and which could also be a function of age, and thus, experience. This would result in the weaker and disadvantaged individuals falling behind and eventually dropping out at the first possible stopover habitat in order to replenish their energy stores. We termed this idea—"*the dropout hypothesis*", similar to the "*rivet hypothesis*" by Ehrlich and Ehrlich (1981), wherein the authors likened species to rivets in an airplane and that there is a limit to how many rivets can be lost before the whole ecosystem collapses. Similarly, we reasoned that avian populations that have to migrate across extensive ecological barriers are dependent on critically located stopover sites that allow them to refuel before or after the barrier. The proximity of the stopover site to the barrier will ensure maximum survival in the population by giving the weaker and inexperienced individuals a chance to accomplish the crossing with greater ease and increased safety. Conversely, the loss of a critically located stop-over site could result in a high mortality rate in the population, which could in the aftermath of a stochastic event result in mortality

rates that exceed the availability of birds for the annual recruitment leading to population declines.

Eilat, Israel, situated at the northern edge of the combined Sahel, Sahara, and Sinai deserts, is reached after a long and arduous journey. Eilat is located at the southern tip of the Arava Valley, i.e. the section of the Rift Valley between the Red and Dead seas. The region is mostly desert, as defined by annual rainfall (Miller, 1961), but in recent decades human settlements were established along the western side of the valley. These are agricultural settlements that have created green areas in the desert. Many spring migrants returning from their wintering grounds in Africa to the Palearctic breeding grounds are unable to store enough energy to complete the migration without refueling at Eilat (e.g. Yosef and Tryjanowski, 2002a, b; Yosef et al., 2002). One such species is the European Bee-eater (*Merops apiaster*). This has allowed us to evaluate the decisions made in migratory flocks of Bee-eaters as they come off the desert migration and must stopover in order to replenish their energy stores. To test our drop-out theory we tested the nonexclusive, working hypothesis that the relative body mass, and consequently body condition, of the individuals would force the lightest ones to stop first and an increasing trend in body mass would be detected northwards. Further, we hypothesized that age would play an important role and that the more experienced adults would cover greater distances at reduced energy costs and that this would result in juveniles dropping-out earlier than the adults. Thus, we predicted that the juveniles with the lowest body mass would be the first to stop at Eilat and that progressively as we go northwards we would find heavier individuals and a larger proportion of adults at the settlements that are closest to the Dead Sea in the north.

2. Study area and methods

It is estimated that more than half a billion birds from Europe and Asia migrate annually through the Middle East (Shirihai, 1996). Israel, located on the only land bridge between Eurasia and Africa, is a junction for birds migrating south in autumn and north to their breeding grounds in spring (Safriel, 1968; Shirihai et al., 2000). In autumn, southbound birds migrate over a broad front. In spring, the Red Sea and the Gulf of Aqaba act as a long deflection barrier forcing northbound birds to concentrate in a very narrow area over the Eilat region (Shirihai, 1996). Also, Eilat is situated at the northern edge of over 2000 km of continuous Sahel, Sahara and Sinai deserts. However, to the north-northeast there are still 650 km more of the Syrian Desert, and due east the vast Arabian Desert. Hence many birds land in the Eilat area in autumn to rest before or in spring after crossing the deserts (Safriel, 1968; Yom-Tov, 1993).

Since the early 1950s agricultural settlements were established in the Arava region. Agriculture has been their mainstay but this massive intrusion into the desert by people and their settlements has led to extreme changes in the water balance and subsequently in the flora and fauna of the region (Yom-Tov and Ilani, 1987). In recent decades, as a result of the climate, the Arava Valley (i.e. the section of the

Syrio-African Rift Valley located between the Dead and Red Seas) became a region where agriculture could be pursued year-round (our personal observations). Some agricultural activities have resulted in outright conflicts between farmers and wildlife, causing the latter to be regarded as "agricultural pests" that must be restrained.

The European bee-eater is a very common migrant on both passages but especially numerous in spring, peaking during late-April; this late date suggests that populations passing through Eilat are from the east and north of the species' range in Eurasia where they are known to breed 2–3 weeks later than in the south-west (Shirihai, 1996). To date we have studied Bee-eaters in the fields of several Kibbutzim—Eilat (29°33.77′N, 34°57.79°E), Roded Farm (29°37.33′N, 34°59.89′E), and Grofit (29°56.16′N, 35°03.63′E), and the Moshavim Ein Yahav (30°39.44′N, 35°13.96′E) and Hazeva (30°46.09N, 35°16.24′E) . Their relative distances from the southernmost point of the study, Eilat, are 9, 44, 125, and 139 km, respectively.

We set mist nets in front of the beehives in each of the afore-mentioned locations in watermelon (Citrullus lanatus) fields in order to catch bee-eaters (Yosef, 2004). The number of bee-hives set up by the farmers for pollination ranged from 6 to 11 as a function of the size of the field and the intensity of the pollination required. However, we do not consider differences in the numbers of hives to have influenced the sex and age composition of the migratory flocks. In all locations we used 6 m mist-nets set up in front and on both sides of the hive. Trapping occurred from 0700 h till the bee-eaters ceased their foraging activity (avg. $4.8 + 2.1$ h/d, $N = 625$ d). All birds trapped were individually ringed, measured (wing chord and tail length), and weighed. In order to prevent their return to the study area, all trapped bee-eaters were released at a distance of a minimum of 35 km from the site in the direction of their migration, i.e. to the south in autumn and north in the spring (Yosef, 2004).

All birds were sexed and aged based on the colors of the greater- and median-coverts (Baker, 1993). Birds older than their first summer were defined as adults. The males have a uniform rufous-chestnut outer web in the greater coverts, and the median coverts are uniform rufous-chestnut. The outer web of the greater coverts of the females has a greenish-blue leading edge, and the median coverts are similar to the males but mostly mixed with green. In juveniles all of the adults' rufous-chestnut are suppressed by green, the V-marks on the scapulars and the back is light green. Ageing was also based on eye color with adults having bright red eyes and juveniles have grayish-red or olive-red iris. However, for the final analysis, we grouped the data into two age groups, juveniles (defined as the second calendar year birds) and adults (older than the second calendar year), but not by sex because the sexing of juveniles was found to be unreliable based on biometrics (RY, unpubl. data).

Flattened maximum wing chord and tail were measured using a wing-ruler (± 1 mm), and body mass was determined with a Pesola 50-g (± 0.5 g) spring balance.

2.1. Statistical analysis

European Bee-eaters are migratory, so their body mass, and possibly also wing length, is likely to fluctuate considerably with season, or on a much larger time scale.

It is also likely that juveniles are smaller than adults. Therefore within the data there were potentially compound effects of age, locality, season and time. As not all birds were sexed, we only defined an age factor with two categories—(i) adult and (ii) juvenile.

We used only data from spring and summer (all captures before 15 May) based on the species' migratory behaviour (Morgan and Shirihai, 1997).

In order to avoid pseudoreplication only data from the first captures were used to calculate the biometrical characteristics.

An ANOVA was used to test for differences in wing length and body mass with age, locality and year.

Using wing length as a measure of body size, we found that body mass was linearly related to wing length ($r_{2418} = 0.241$, $p < 0.0001$). Accordingly, we took the ratio of body mass to wing length as a measure of body condition, thereby adjusting body mass for the effect of body size (Brown, 1996). An ANOVA was used to test for differences in body condition with age, locality, season and year.

All interaction terms were considered within the ANOVA models and if they were found to be insignificant they were removed prior to testing the main effects.

Average values are presented as means ± 1 S.D. We chose $p < 0.05$ as the minimum acceptable level of significance.

The analyses were carried out using the statistical package SPSS Inc, Chicago.

3. Results

During the spring migration of the five years, 1999–2003, of our study we trapped and ringed 2418 Bee-eaters (avg. 477 ± 449, range 94–1244). Of these, from south to north (Fig. 1), 119 (5.0%) were caught at Eilat, 399 (16.7%) at the Roded Farm, 1556 (65.2%) at Grofit, 192 (8.1%) in Ein Yahav, and 152 (6.4%) in Hatzeva. The number of retraps within the season was negligible. Only three birds (0.1%), of the Bee-eaters released at the Bird Sanctuary of the IBRCE in Eilat, returned to the foraging sites at which they had been trapped. No Bee-eaters were retrapped in the region between the seasons or years of this study.

Age composition: The age composition of the birds caught during the study differed significantly between study sites (Fig. 1. $\chi^2 = 169.6$, df = 4, $p < 0.001$). The number of juveniles decreased as the distance from the desert edge increased. The mean number of juveniles equalled 41.9%, but ranged from a high of 73.1% in Eilat to a low of 11.2% in Hazeva.

Biometrics: *Wing length* was recorded for 2386 Bee-eaters. Wing length varied significantly between years ($F_{4,2385} = 14.40$, $p < 0.0001$), with age ($F_{1,2385} = 25.33$, $p < 0.0001$) and with locality ($F_{4,2385} = 99.19$, $p < 0.0001$). However, the last relation is especially of interest because wing length systematically increased for both age categories, when effect of year was controlled (Fig. 2).

Also the interactions between age, locality and year on European Bee-eater wing length were significant (all $p < 0.02$, excluding insignificant interactions year*age, at
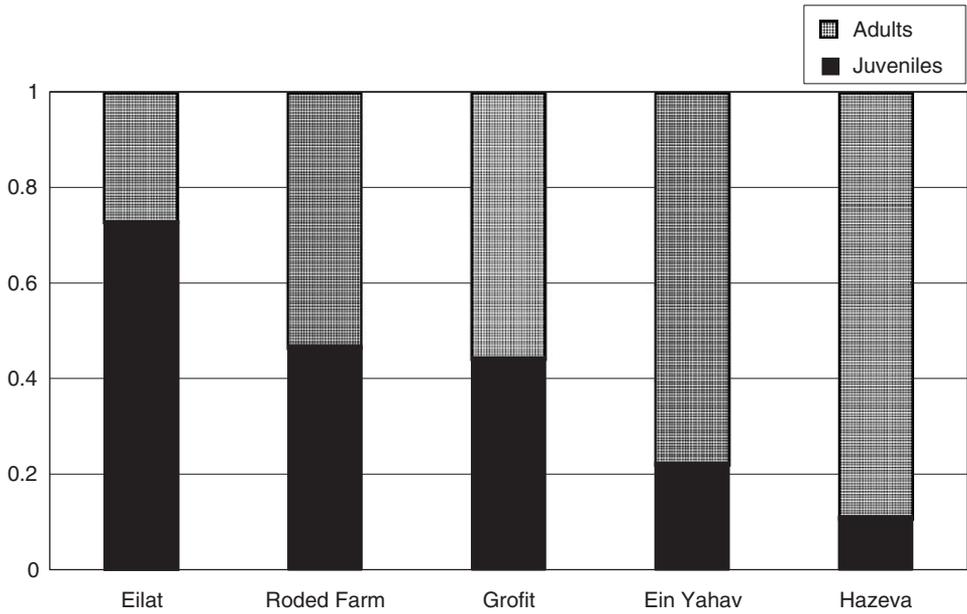
Fig. 1. The relative percentages of juvenile: adult migratory European Bee-eaters (*Merops apiaster*) trapped from south to north in the Arava Valley, Israel.
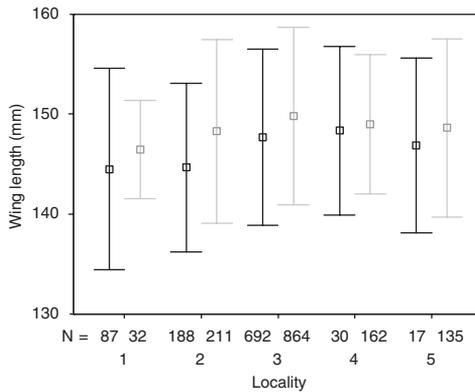

Fig. 2. Differences in mean wing length between the five study sites for adults (dotted line) and juveniles (solid lines). Difference between localities was significant for both age categories—for statistical tests see text. The sites are numbered from south to north—see Study site. Sample sizes (left number—juveniles, right—adults) are provided under *x*-axis. Data are presented as means ± S.D.

$p = 0.206$ and year*locality, at $p = 0.110$). All controlled sources explained 21.4% of variation in wing length.

Adult wing lengths were on average 2–3 mm longer than juvenile wing lengths; there was, however, considerable overlap between the age categories.

Body mass was recorded for 2386 Bee-eaters. Body mass varied significantly between years ($F_{4,2385} = 27.66$, $p < 0.0001$), with age ($F_{1,2385} = 4806.50$, $p < 0.0001$) and with locality ($F_{4,2385} = 106.25$, $p < 0.0001$). Similar to the wing length data, of special interest was the last relationship wherein body mass systematically increased for both age categories, when other effects were controlled. The relationship was especially strong for the juveniles (interaction age*locality significant at $p < 0.0001$).

Also other interactions between age, locality, and year on European Bee-eater body mass were significant (all $p < 0.001$, excluding three-way insignificant interaction locality*year*age at $p = 0.272$). All controlled sources explained 63.9% of variation in body mass.

Adults were on average 6–7 g heavier than juveniles; there was, however, considerable overlap between the age categories (Fig. 3).

Body condition index was established for 2386 Bee-eaters. Body condition varied significantly between years ($F_{4,2385} = 7.04$, $p < 0.0001$), with age ($F_{1,2385} = 466.06$, $p < 0.0001$) and with locality ($F_{4,2385} = 9.09$, $p < 0.0001$). Similar to the fore-mentioned parameters, body condition increased with distance from Eilat in the south to the north. The relationship was much stronger for juveniles (interaction age*locality significant at $p < 0.0001$). Pattern of changes in condition index was extremely similar to changes in body mass, because both measures strongly intercorrelated ($r = 0.941$, $p < 0.0001$, $n = 2418$).

Also other interactions between age, locality and year on European Bee-eater body condition were significant (all $p < 0.0001$, excluding locality*year at $p = 0.162$, and three-way insignificant interaction locality*year*age at $p = 0.280$). All controlled sources explained 54.6% of variation in body mass.

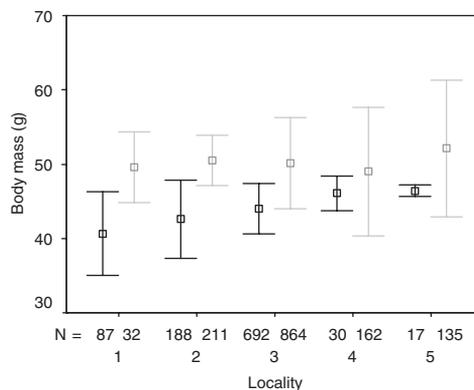Adults were on average in better condition than juveniles (differences ca. 10% in body condition index).

Fig. 3. Differences in mean body mass between the five study sites for adults (grey lines and boxes) and juveniles (black lines and boxes). Difference between localities was significant for both age categories—for statistical tests see text. The sites are numbered from south to north—see Study site. Sample sizes (left number—juveniles, right—adults) are provided under the x-axis. Data are means±S.D.

4. Discussion

Migratory stopover is an important component of the migratory phase of the life history cycle of the migratory species and are made to restore energy reserves or physiological imbalances and to avoid flying at certain times of day or night, in inclement weather, or infavorable winds (Karasov and Pinshow, 1998). To date most of the studies have related to the ecology, timing, feeding, vigilance, physiology, phenology, and local environmental factors (cf. Biebach, 1995; Karasov and Pinshow, 1998; Gannes, 2001). In this paper we explain what we consider to be one of the major considerations, body condition, that forces migratory birds to choose their stopover site and that is explained by the "dropout hypothesis".

The energy considerations suggest that many of the species undertake a non-stop trans-Saharan flight rather than a series of short flights with stopovers in the desert (Wood, 1992; Yom-Tov, 1993). The data confirm our predictions that the European Bee-eaters in the worst body condition were the first to drop out at Eilat immediately after the crossing of the combined ecological barrier of the North African deserts of the Sahel, Sahara and Sinai. Hence, a trend of increasing body mass northwards illustrated that birds dropped out of the advancing flock as a function of decreasing body condition and the attractive appearance of green patches on the ground on their flyway.

It is possible that birds dropped out of the flock(s) before or after the geographical limits of the study area, i.e. south of Eilat in the Sinai Peninsula, Egypt, or north of Ein Yahav. It is also possible that at any location included in the study, the body condition of the population that decide to drop out at that point will vary from year to year and will depend on the variability of the local environmental factors. However, we consider these considerations to be irrelevant to the larger picture that comprises our "drop-out hypothesis."

Another possibility that cannot be ruled out is prior experience. It is possible that adults in the past experienced better conditions in the more northern locations and make a special effort to reach these areas where food resources are abundant and competition is low. However, we agree with Shochat et al. (2002) who concluded that the birds possess imperfect knowledge, and certainly not updated in experienced adults, of resource dependence and that lead to free, but not ideal distributions of migrant birds in unfamiliar stopover sites. This is substantiated by the fact that although we have worked at the Roded Farm and Grofit for all of the years included in the study, only three of the birds were retrapped between seasons or years.

The importance of this study, and the dropout hypothesis, is to stress a major conservation problem that occurs at many staging areas wherein modern human practices have resulted in fragmentation or incomplete loss of the habitat for migratory species, and there is a need for restoration of natural areas and corridor zones. In this case, the birds are assumed to be unable to discern habitat quality or conspecifics density (cf. Shochat et al., 2002) at the chosen site when they decide to drop out from the moving flock. The fate of these birds will largely be dictated by whether there are enough resources for them to replenish their body energy, or to move away from the area if there are not enough resources, or if the competition is

such that it prevents their access to the desired resource. Hence, in areas known to be important stopover sites for migratory populations, an effort should be made to not only conserve the major site but also corridors leading from it in the direction of the migrations (Williams et al., 2003). The requirements of the migrants, and the resources available, dictate acquisition rates of body stores and the stopover length and are capable of influencing the overall migration time and influence the subsequent arrival at the breeding grounds (Alerstam and Lindstrom, 1990). The conservation consequences for the Eilat/Aqaba region are far reaching because in the spring migration it is reached after the desert crossing and most of the area has already been taken up for human purposes and little of the original habitats remain (Rosenzweig, 2003).

Our data support our "drop-out hypothesis." The weaker birds dropped out at the first stopover point, Eilat, immediately after crossing the deserts of Sahel, Sahara and Sinai in the spring. The relative body condition of the birds trapped to the north increased with growing distance from Eilat also supporting the idea that individuals in better condition will try to optimize the migratory distance covered by maximizing the distance covered prior to their being forced to stop to refuel. Experience also appears to play an important role and an incremental increase in the relative proportion of adults increased as we progressed to the north. Our data stress the importance of stopover sites such as Eilat for migratory species. The survival rate of the disadvantaged juveniles, that are the future recruitment potential of the breeding population, would be greatly decreased if the stopover sites at which they must refuel are damaged or destroyed, and alternative sites are not made available for the birds to improve their body condition and to ensure their continued migration to the breeding grounds to the north across Europe and Asia.

We conclude that present and future planning must take into consideration the conservation aspects of the stopover sites of the migratory bird populations that traverse the Eilat and Aqaba region, and northwards along the Arava Valley in order to ensure the survival of the migratory populations. In a wider perspective, the conservation concept of staggered stopover sites should also be applied to the other regions and countries that share the Syrian-African Rift Valley in order to ensure the continued migrations of the hundreds of millions of birds that avail of these sites twice a year.

References

Alerstam, T., Lindstrom, A., 1990. Optimal bird migration: the relative importance of time, energy, and safety. In: Gwinner, E. (Ed.), Bird migration, Physiology, and Ecophysiology. Springer, Berlin Heidelberg, pp. 331–351.

Baker, K., 1993. Identification guide to European non-passerines. BTO guide 24. British Trust of Ornithology, Thetford.

Biebach, H., 1995. Stopover of migrants flying across the Mediterranean Sea and the Sahara. Israel Journal of Zoology 41, 387–392.

Biebach, H., Friedrich, W., Heine, G., 1986. Interaction of bodymass, fat, foraging and stopover period in trans-Sahara migrating passerine birds. Oecologia 69, 370–379.

Brown, M.E., 1996. Assessing body condition in birds. Current Ornithology 13, 67–135.

Carmi, N., Pinshow, B., Porter, P., Jaeger, J., 1992. Water and energy limitations on flight duration in small migrating birds. Auk 109, 269–276.

Ehrlich, P.R., Ehrlich, A., 1981. Extinction: the causes and consequences of the disappearance of species. Random House, New York.

Fransson, T., 1998. , Patterns of migratory fuelling in Whitethroats *Sylvia communis* in relation to departure. Journal of Avian Biology 29, 569–573.

Gannes, L.Z., 2001. Comparative fuel use of migrating passerines: effects of fat stores, migration distance, and diet. Auk 118, 665–677.

Karasov, W.H., Pinshow, B., 1998. Changes in lean mass and in organs of nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiological Zoology 71, 435–448.

Liechti, F., Bruderer, B., 1998. The relevance of wind for optimal migration theory. Journal of Avian Biology 29, 561–568.

Miller, A.A., 1961. Clilmatology. Methuen, London.

Morgan, J.H., Shirihai, H., 1997. Passerines and Passerine migration in Eilat 1984–1993. International Birdwatching Centre, Eilat.

Nolet, B.A., Drent, R.H., 1998. Bewick's Swans refueling on pondweed tubers in the Dvina Bay (White Sea) during their spring migration: first come first served. Journal of Avian Biology 29, 574–581.

Pennycuick, C.J., 1989. Bird Flight Performance: a Practical Calculation Manual. Oxford University Press, Oxford.

Rosenzweig, M.L., 2003. Win-win Ecology: How the Earth's Species can Survive in the Midst of Human Enterprise. Oxford University Press, Oxford.

Safriel, U., 1968. Bird migration at Eilat, Israel. Ibis 110, 283–320.

Shirihai, H., 1996. The birds of Israel. Academic Press, London.

Shirihai, H., Yosef, R., Alon, D., Kirwan, G., Spaar, R., 2000. Raptor migration in Israel and the Middle East—a summary of 30 years of field research. International Birding & Research Center in Eilat, Israel.

Shochat, E., Avramsky, Z., Pinshow, B., Whitehouse, M.E.A., 2002. Density-dependent habitat selection in migratory passerines during stopover: what causes the deviation from IFD? Evolutionary Ecology 16, 469–488.

Weber, T.P., Ens, B.J., Houston, A.I., 1998. Optimal avian migration: a dynamic model of fuel stores and site use. Evolutionary Ecology 12, 377–401.

Williams, J.C., ReVelle, C.S., Bain, D.J., 2003. A decision model for selecting protected habitat areas within migratory flyways. Socio-Economic Planning Science 37, 239–268.

Wood, B., 1992. Yellow Wagtail *Motacilla flava* migration from West Africa to Europe: pointers towards a conservation strategy for migrants on passage. Ibis 134 (suppl.), 66–76.

Yom-Tov, Y., 1993. The importance of stopover sites in deserts for Palearctic migratory birds. Israel Journal of Zoology 39, 271–273.

Yom-Tov, Y., Ilani, G., 1987. The numerical status of *Gazella dorcas* and *Gazella gazella* in the southern Negev Desert, Israel. Biological Conservation 40, 245–253.

Yosef, R., 2004. Resolving the apiculture and migratory bee-eater (*Merops apiaster*) conflict in the Arava valley, Israel. Advances in Vertebrate Pest Management 3, 117–122.

Yosef, R., Tryjanowski, P., 2002a. Differential spring migration of Ortolan Bunting *Emberiza hortulana* by sex and age at Eilat, Israel. Ornis Fennica 79, 173–180.

Yosef, R., Tryjanowski, P., 2002b. Avian species saturation at a long-term ringing station—a never-ending story? Journal of Yamashina Institute of Ornithology 34, 89–95.

Yosef, R., Tryjanowski, P., Bildstein, K., 2002. Spring migration of adult and immature buzzards (*Buteo buteo*) through Eilat, Israel: timing and body size. Journal of Raptor Research 36, 115–120.

Yosef, R., Fornasari, L., Tryjanowski, P., Bechard, M.J., Kaltenecker, G.S., Bildstein, K., 2003. Differential spring migration of adult and juvenile Levant Sparrowhawks (*Accipiter brevipes*) through Eilat, Israel. Journal of Raptor Research 37, 31–36.